STUDIES OF THE FORAGING BEHAVIOUR, ACTIVITY PATTERNS AND COMMUNITY STRUCTURE OF BUMBLEBEES (BOMBUS SPP.) POLLINATING FIELD BEANS (VICIA FABA) AND PHACELIA (PHACELIA TANACETIFOLIA) IN EASTERN SCOTLAND

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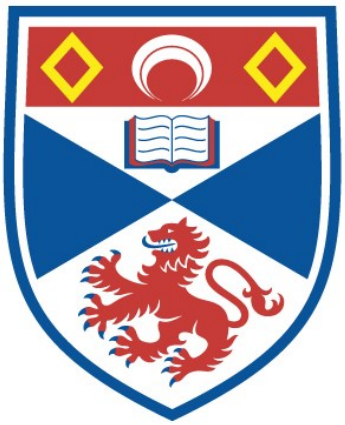

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Studies of the foraging behaviour, activity patterns and community structure of bumblebees (*Bombus* spp.) pollinating field beans (*Vicia faba*) and phacelia (*Phacelia tanacetifolia*) in eastern Scotland

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Abstract

The nectar profiles of twelve cultivars of field bean (*Vicia faba*), and of *Phacelia tanacetifolia* in eastern Scotland were analysed in relation to climatic variables. Observations were made of the activity patterns of *Apis mellifera* and six species of bumblebees on the experimental cultivars of *V. faba* and on a large commercial crop of *Phacelia*. Foraging behaviour and flower visitation rates were analysed in relation to bee species, nectar rewards and to the architecture of the crop. The species composition of the bee communities on *V. faba* and *Phacelia* was recorded during timed walks and is discussed in relation to floral structure and to interspecific differences among bumblebees. Scientific literature relating to the pollination of field beans is reviewed in detail.

Contents

Chapter 5: General discussion

Introduction, part I

The pollination of field beans *Vicia faba* A review of the literature

1.1 Pollination, fertilisation and yield of field beans

The faba bean, *Vicia faba* (see Plate 1), belongs to the pea family or Fabaceae (Hutchinson 1973). It is the sixth most important pulse crop in terms of global production, and has been an important component of world agriculture for at least 4,000 years. It remains an important food crop in North Africa and the Middle East, and many European countries use it as a source of vegetable protein for animal feed. Cultivation in the UK has become less intensive due to the greater economic reward, reliability and productivity of crops such as oilseed rape (Stoddard & Bond 1987). The two forms of the faba bean (broad beans *V. faba major*, and field beans *V. faba minor*) differ mainly in the size of the seed, that of broad beans being larger. Much of the literature surrounding the subject of fertilisation and yield dates back to the 1950's. This survey focuses on the factors influencing seed production in *V. faba*.

V. faba crops often have low and unpredictable yields. A large proportion of flowers and young pods are frequently shed (Drayner 1959); this may be due to inadequate nutrition, low light levels or inadequate cross-pollination (Soper 1952). In commercial fields of winter beans grown in Cambridgeshire in the early 1980s, the mean maximum number of pods held on any flowering node exceeded one in only five of twenty-one fields (Stoddard 1986a). Soper (1952) quotes mean harvest figures of only 6.5, 11.1 and 8.8 pods per plant. These figures are startlingly low considering that each flowering node on a field bean plant can bear, on average, between five and eight flowers, and each flower has the potential to develop into a seed pod.

V. faba is one of the few agricultural crops primarily dependent on wild vectors for pollination, and consequently yields can vary greatly from year to year (Stoddard & Bond 1987). Observations of the importance of bees as pollinators for *V. faba* were first published by Charles Darwin in the Gardener's Chronicle of 1858, and subsequent research has demonstrated that pollination and yield can be improved by the attentions of sufficient numbers of bees (Kendall & Smith 1975).

Bees are attracted to the highly fragrant, zygomorphic flowers of *V. faba*. Flowers must be "tripped" in order for fertilisation to take place. "Tripping" occurs when pressure upon the standard petal forces the stigma downwards to brush against pollen contained on the anthers (Free 1993), and occurs in response to disturbance of the petals such as the entry of an insect into the flower. It can be effected by insect visitors or by manipulation of the flowers (known as manual tripping). For cross-pollination to occur, pollen must be transferred onto the body of a visiting insect. Long-tongued bumblebees are generally recognised as being the most efficient cross-pollinators, but insect visits can also promote autofertilisation (Hanna & Lawes 1967). In the absence of tripping, a moderate amount of self-fertilisation can take place, since pollen stored in the keel of the flower may fall onto the stigmatic surface. Differences in the potential for autofertility among genotypes and cultivars of *V. faba* may be based in phenotypic differences in floral structure and the quantity of pollen, which affect the mechanics of pollination and selfing (Kambal et al 1976). This may help to explain why different genotypes and cultivars show different degrees of response, in terms of seed yields, to insect pollination (Hanna & Lawes 1967; Free & Williams 1976; Stoddard 1986a). Although *V. faba* sets seed readily by enforced self-pollination, crossbred plants show greater vigour (Fyfe & Bailey 1951) and

crossbred seeds are more frost-resistant (Free 1993). Bees are not essential for fertilisation to take place, but they are necessary to ensure maximal pollination and to improve yields.

Field bean crops are midway between the extremes of cross-fertilising and self-fertilising (Fyfe & Bailey 1951), and show a marked expression of hybrid vigour (Stoddard & Bond 1987). Hybrid plants have increased self-fertilisation abilities, while many inbred plants set no seed at all unless tripped. The dependence of seed-set on tripping is far more marked in inbred plants (Drayner 1959). Estimates of the proportion of natural cross-fertilisation in a bean crop agree that roughly one third of plants in any crop are hybrids, i.e. grown from cross-pollinated seed, and two thirds are inbred, i.e. grown from self-fertilised seed (Fyfe & Bailey 1951; Rowlands 1958; Drayner 1959; Riedel & Wort 1960; Hanna & Lawes 1967; Kendall & Smith 1975).

The faba bean breeding system combines the evolutionary flexibility of cross-pollination with the ability to survive seasons in which pollinators are scarce. The autofertility of hybrid plants ensures a moderate seed yield in unfavourable conditions (Drayner 1959). The resulting plants, however, are inbreds that set little or no seed (Free 1993). After a few generations of self-fertilisation, plants demonstrate inbreeding depression and a greatly reduced yield. *V. faba* experts notice that inbred lines tend to produce large numbers of scented flowers, while highly outcrossed lines tend to have smaller numbers of less fragrant flowers (Gavin Ramsay, S.C.R.I., personal communication). This may be an Evolutionary Stable Strategy on the part of the plant to avoid the extremes of homozygosity or heterozygosity that may result from many consecutive generations of selfing or outcrossing. Most commercial *V. faba* seed does not consist of two well-defined 'hybrid' and 'inbred' types, but of a more heterogeneous mixture showing a range of different degrees of autofertility, so that crops will vary in their ability to set seed (Kendall & Smith 1975). The proportions of cross-bred and self-fertilised seed obtained from *V. faba* crops may also vary between fields, years and localities (Bond & Pope 1974).

Flowers on the upper nodes are more autofertile than those on the lower nodes. Stoddard & Bond (1987) suggest that the upper flowers are more likely to be self-pollinated because they flower later in the season when the floral display has declined and bee visitation is lower. Bees pollinating the earlier flowers, i.e. those borne on

the lower flowering nodes, produce greater seed set than in later flowers, i.e. those on the upper nodes (Riedel & Wort 1960; Wafa & Ibrahim 1959; Free 1966; Hanna & Lawes 1967; Kendall & Smith 1975; Free & Williams 1976). When pollinating insects are excluded from the lower nodes there is usually a compensating increase in pod production on the more autofertile upper nodes. The even ripening and harvesting of a field bean crop are dependent on adequate pollination of the lower nodes (Stoddard & Bond 1987).

Agricultural methods and environmental conditions have a vital impact on field bean yields. Farming techniques, soil moisture and fertility, weather conditions and the adequacy of insect-mediated cross-pollination determine the level of pod-set in a normal crop. Plant density and the incidence of plant disease also influence pod-set (Soper 1952). At high planting densities, plants suffer from competition for space, nutrients, water, light etc., and there is a reduction in the number of flowering nodes, the number of flowers on each inflorescence, and in pod production by the plant as a whole, particularly on the lower nodes (Hodgson & Blackman 1956). Irrigation may increase the percentage of fertilised ovules that actually develop into seeds (Stoddard 1986b).

Field size may influence *V. faba* yields indirectly, through pollination. Seed yields from individual plants have been observed to be greater at the edges of fields than in the centre. This may be because bumblebees and other pollinators have greater access to plants at the edge of the field (Free & Williams 1976) or because the lower plant density at the edge of the field permits a higher survival rate for seed embryos produced by self-pollination (Bond & Pope 1974). Whether self-fertilised seeds are allowed to mature or are aborted by the plant depends mainly on plant density (Stoddard 1986b).

Each flower has the potential to develop into a seed pod, therefore the potential for seed production by any individual plant is limited by the number of flowers. Early sowing combined with the use of fertilisers will produce the maximum number of flowers without affecting the ratio of seeds to flowers (Hanna & Lawes 1967). The timing of the flowering season is affected by sowing date (Stoddard 1986a). If beans flower too early, there may not be sufficient pollinators yet active to achieve full pollination. This is why winter varieties of field beans tend to be planted in Southern

Britain, where bees are active earlier in the season (Gavin Ramsay, personal communication).

Little is known of the quantitative relationship between the abundance of pollinators and seed production. The potential for yield improvement is demonstrated by the low yields of some commercial crops (Stoddard 1986a), and by the fact that the yields of individual flowers can be experimentally increased by manual tripping (Free & Williams 1976). Pollination by bees improves pod-setting and growth so that pods mature more rapidly (Wafa & Ibrahim 1959). Actual numbers of bees may be limit pollination, particularly in early crops (Stoddard 1986) and in large fields (Bond & Pope 1974; Free & Williams 1976). For some crops (e.g. red clover *Trifolium pratense* pollinated by *Bombus fervidus*) the degree to which pollinators move between plants and the extent of pollen carryover are determining factors in seed set (Plowright & Hartling 1981).

The mean incidence of floral fertilisation can vary widely between fields and from year to year (Stoddard 1986a & 1986b). This may reflect spatial and seasonal variations in pollinator populations. Insect pollination, however, does not always lead to fertilisation, and fertilisation does not always lead to fruiting (Stoddard & Bond 1987). Flowers on the more autofertile upper nodes are less likely to develop into pods because self-fertilised embryos are more likely to be aborted. Within an inflorescence, the proximal flowers are more likely to develop into pods because of their protected position (Smith 1982).

1.2 Local and geographical variation in field bean pollinator communities

The wide geographical range of *V. faba* suggests that there must be flexibility in the plant-pollinator relationship. Only long-tongued bees can reach the nectar via the mouth of the corolla. Bees of the families Apidae, Anthophoridae and Andrenidae are the most economically important pollinators of faba beans world-wide (Stoddard & Bond 1987). There are geographical, regional and seasonal variations in field bean pollinator communities due to variation in habitat type, and in the dates and duration of flowering at different sites and in different years. For example, the communities of pollinators in four areas of Egypt differed widely in species composition, and were

significantly poorer in areas that had suffered from extensive land disturbance (Wafa & Mohamed 1970). Insect populations fluctuate widely in time and space, but climatic conditions and the availability of forage and suitable nesting sites are of paramount importance.

Field bean crops in the UK are pollinated by long-tongued bumblebees (such as *B. pascuorum* and *B. hortorum*) and honeybees (Free 1993; Stoddard & Bond 1987). Three broad categories of flower-visitation behaviour are recognised throughout the present thesis. These are:

- Positive flower visits (i.e. visits to the front of the flower involving entry into the mouth of the corolla tube and contact with the sexual structures)
- Negative flower visits (i.e. nectar robbing, either primary or secondary)
- Visits to extrafloral nectaries

Short-tongued bumblebees may make positive visits when they are in search of pollen, but are also common as nectar robbers. They pierce the base of the corolla tube with their mandibles, obtaining access to the nectar without having to enter the flower. "Illegitimate" foraging may be effected by primary robbers (those that pierce the corollas) or by secondary robbers (individuals exploiting pre-existing holes), and bypasses the sexual parts of the flower (Free 1993). Honeybees may become habituated to taking nectar through holes pierced by robber bumblebees, so that the value of managing hives for *V. faba* pollination is doubtful in areas where short-tongued bumblebees are common (Stoddard & Bond 1987).

Egyptian crops of faba beans flower between mid-December and the first half of February. They are pollinated by a variety of insects, mainly five species of anthophorid, characterised by long proboscides, furry bodies, relatively high body weight and high flower-visitation rate (Wafa & Ibrahim 1959). The mason bee *Chalicodoma sicula* and the carpenter bee *Xylocopa aestuans* are also effective pollinators. Honeybees are extremely abundant in Egypt (Wafa & Ibrahim 1959), but on a local scale solitary bee species may be more abundant and important in pollination (Free 1993).

In New Zealand, the field bean flowering season takes place in early spring. The short-tongued bumblebee *B. terrestris* is active at this time, but is not effective as a pollinator since it often robs the flowers (Free 1993). Since the long-tongued *B.*

ruderatus and *B. subterraneous* do not become active until after *V. faba* has finished flowering, Free suggests introducing *B. pascuorum* or *B. hortorum* to New Zealand in the hope that they might establish perennial colonies. Other sources state that *B. hortorum* was already well established in New Zealand by the early 1980's (Newton & Hill 1983). In Australia in 1987 feral honeybees were the only wild pollen vectors observed to be visiting *V. faba* , and in Canada solitary bees and bumblebees are important (Stoddard & Bond 1987).

The species composition of field bean pollinator communities is highly variable even within Europe. Honeybees comprised 80% of the bee visitors to *V. faba* crops in one study in France (Tasei 1976); however they only pollinated on 5-20% of their visits, as most individuals were robbing nectar. *B. hortorum*, *B. ruderatus*, *Anthophora* spp. and *Eucera* spp. pollinated on all visits, but were far less numerous on the crop. A study of field bean crops in Denmark showed daily and seasonal variation in pollinator behaviour (Poulsen 1973). The most abundant foragers were honeybees. Bumblebees were considerably less numerous, and of the five observed species the most common one, *B. terrestris*, was mainly engaged in nectar robbing.

The causes of temporal and spatial variations in pollinator communities on field beans within the UK may be summarised as follows:

- Variation in the suitability of agricultural sites and their surroundings for bumblebee nest sites (Free & Williams 1976).
- Variation in the regional and local distribution of honeybee hives.
- Variations in the flowering seasons of *V. faba* in different parts of the country and according to farming practice (Stoddard 1986).
- Temporal and spatial change in the regional and local distributions of effective pollinating species (Williams 1982 & 1986).
- Regional and seasonal differences in the timing of the life cycles of pollinating species, which may vary along geographic clines (Prys-Jones & Corbet 1987). Bee species differ in their behavioural and developmental responses to long-term and short-term changes in climate (see Section 1.11), so that pollinator communities fluctuate on an hourly, daily and seasonal basis.

1.3 Bumblebees on field beans

Bumblebees and field beans are popular subjects in many areas of research, including neurobiology, ecology, agriculture, physiology and genetics, but few researchers have focused their attention on the dynamics of the relationship between the two. Attempts to assess the value of different bee species as pollinators for *V. faba* have produced contradictory results. Free (1966) found that plants contained in cages to which honeybees were allowed access for only one hour each morning produced higher yields than plants in insect-free cages, in which only self-pollination occurred. Plants in open plots, however, produced the greatest seed yield in all yield components. Free concluded that "*the large differences between plants caged with bees and in open plots probably results from the effects of the cages themselves*". Higher yields in open plots may, however, have more to do with the accessibility of uncaged plants to long-tongued bumblebees.

Field beans receive most of their insect visitors during the afternoon (Stoddard and Bond 1987; Juliet Osborne, personal communication). Most honeybee visits are made in the afternoon during the period of anther dehiscence (Stoddard & Bond 1987). Pollen-collecting honeybees can bring about pollination, while those taking nectar from extrafloral nectaries or corolla piercings generally do not (Free 1962).

The main approaches used in studies of the relative pollinating efficiency of different bee species on field beans can be broadly subdivided into three categories:

- Caging experiments
- Counts of relative abundance
- Recording insect visits, marking flowers and measuring subsequent yields

The latter approach was used by the Institute of Arable Crop Research at Long Ashton Research Station (Bristol University) between 1972 and 1974. By examining pod-set on marked, visited flowers, Smith (1974) found that long-tongued bumblebees were the most effective pollinators. These were "*not significantly better pollinators per* [flower] *visit than honeybees, but each* [long-tongued] *bumblebee tended to visit more flowers during a given period of time*", therefore "*the relative value of bumblebees and honeybees largely depends on the numbers of each species foraging in the crop*". (Smith et al. 1974). Poulsen (1973) observed that bumblebees were the most rapid foragers on field beans in Denmark.

In their investigations of relative pollinating efficiency, Kendall and Smith (1975), also working at IACR-Long Ashton, focused their research on the lower nodes of the plant, as the lower flowers are crucial for improved yields and early, uniform harvests (Hanna & Lawes 1967; Kendall & Smith 1975). By marking flowers and noting seed production they found the following order of effectiveness: positive visits (by long-tongued bumblebees and by honeybees); manual tripping; negative visits (i.e. robbing) and no visits (i.e. natural self-pollination). Nectar robbing does not prejudice pod development (Newton & Hill 1983) but the pollinating efficiency of a bumblebee community depends on which species are present and their relative abundance. From their observations Kendall & Smith defined a parameter called the Effective Pollination Period (EPP) to estimate the numbers of honeybees and bumblebees per m^2 that would be necessary to pollinate 98% of the early flowers in a faba bean crop over a given time period. EPP can be described as the sterile longevity of the flower minus the time taken by pollen tubes to grow down the style and reach the ovules, and it is influenced by weather, time of day, and nectar availability. For faba beans, the EPP is estimated to be about 6 days. Almost four times as many honeybees as bumblebees would, according to their estimate, be needed to accomplish the same effect.

1.4 The relative efficiency of honeybees and bumblebees as pollinators

Many of the studies of the relative efficacy of bumblebees and honeybees as crop pollinators have focused on deep corolla leguminous crops (Free 1993). Pollinating efficiency is influenced by a host of factors including relative abundance (Free 1968; Kendall & Smith 1975), the number of individuals of each species engaged in different types of flower visitation behaviour (Free 1962; Poulsen 1973; Wratt 1986), the proximity of competing crops (Arretz & Macfarlane 1986) and the prevailing environmental conditions (Hanna & Lawes 1967). The agricultural importance of bumblebees has often been underestimated (Bohart 1960; Willmer, Bataw & Hughes 1994). Colonies of honeybees show large and heritable differences in their tendency to collect pollen from field beans when other crops are in flower (Synge 1947); importing hives to crops in flower continues, however, to be seen as an effective means of improving yields (Free & Williams 1976).

Honeybees may be at least as important as bumblebees in legume pollination in general; for example, honeybees are more effective pollinators for glasshouse crops of runner beans (Free and Racey 1986). Honeybees and bumblebees may be equally efficient on individual field bean flowers (Free 1968; Smith et al 1974; Kendall & Smith 1975), but nectar-gathering bumblebees are more likely to make positive flower visits (Free 1968; Bond & Hawkins 1967; Kendall & Smith 1975), work faster when making positive visits to individual flowers, and tend to visit more flowers per plant (see Section 5.2i). A comparison of the flower-visitation rates of honeybees and bumblebees suggest that the pollinating efficiency of one bumblebee is equal to that of 3-3.5 honeybees (Poulsen 1973; Kendall & Smith 1975).

In general, bumblebees are less flower-constant than honeybees (Free 1970). For this reason bumblebees have been supposed to be more erratic foragers. Lower flower constancy can be advantageous, however, in large fields or in crops where frequent movement between plants promotes cross-pollination and yield. For example, bumblebees move more freely between rows of raspberry (*Rubus idaeus*) plants than honeybees (Willmer et al. 1994). On field beans, bumblebees tend to visit more flowers per foraging trip, and cover a greater area over several trips (Free 1968). Honeybee colonies need to be located close to field bean crops, for the reason that levels of foraging by honeybees decline over increasing distances (up to 800m) from the hive (Free & Williams 1976).

The large, hairy bodies of bumblebees usually carry more pollen than the bodies of honeybees (Free & Williams 1972; Willmer et al. 1994). In addition, the nectar of field bean flowers is more accessible to bumblebees than to honeybees because bumblebees tend to have longer probsocides. For nectar-gathering honeybees it is less energetically expensive (therefore more rewarding) to forage from pre-existing corolla piercings than to enter the mouth of the corolla.

There are few large scale studies of the influence of the activities of different bee species upon field bean yields. Free (1966) found that plants to which bumblebees had access produced more pods per plant, more seeds per pod, and a greater seed mass than plants visited only by honeybees. Bond & Pope (1976) observed no discernible improvement in the crop yields after importation of honeybee hives. A study of hive-supplemented commercial crops of *V. faba* in Southern Cambridgeshire

found a moderate yield improvement in 1982 but not in 1983 (Stoddard 1986). The data in Table 1.1 shows that flowers visited by long-tongued bumblebees had the highest incidence of floral fertilisation and produced the highest yields.

Regime	**Visit type**	**Set***	**Mean no. pods per plant**	**Mean no. seeds per pod**	**Mean seed weight per plant (g)**	**Ref.**
Uncaged			10.2	3.08	21.38	Free ('66)
Caged	none		5.77	2.5	9.97	Free ('66)
Caged	manual tripping	75		3.26		Kendall & Smith ('75)
Caged	none	32.1		3.26		Kendall & Smith ('75)
B. terrestris	unspecified	37				Smith et al. ('74)
B. lucorum	unspecified	45				Smith et al. ('74)
Honeybees	1 positive visit	76.4		3.44		Kendall & Smith ('75)
Honeybees	2 or more positive visits	94.1		3.65		Kendall & Smith ('75)
B. hortorum	positive visits	100		3.63		Kendall & Smith ('75)
B. hortorum & robbers	positive and negative visits	100		3.67		Kendall & Smith ('75)
B. pascuorum	positive visits	81		3.62		Kendall & Smith ('75)
B. pascuorum & robbers	positive and negative visits	100		3.67		Kendall & Smith ('75)
Short-tongued bumblebees	positive visits	76.9		3.70		Kendall & Smith ('75)
Short-tongued bumblebees	negative visits	50.3		3.25		Kendall & Smith ('75)
Caged	manual tripping	75		3.26		Kendall & Smith ('75)
Caged	none	32.1		3.26		Kendall & Smith ('75)

Table 1.1 The influence of various pollination regimes on field bean yields
***Set = the percentage of flowers which develop into seed pods.**

Several authors advocate growing field bean crops in areas where bumblebees are more abundant (Free & Williams 1976). However, many problems are encountered in extrapolating from small scale field studies to crop pollination on a large scale.

The potential value of bumblebees for commercial *V. faba* pollination is very high, but their role in modern cultivation has not been estimated. The small size of bumblebee populations, their vulnerability to vagaries of climate and the recent and continuing decline in the availability of suitable nesting sites decrease their reliability as crop pollinators. Their actual value as pollinators of other leguminous crops is demonstrated in one instance by the fact that agricultural encroachment upon bumblebee habitats in Manitoba, Canada, had an extremely deleterious effect on alfalfa seed yields (Stephen 1955).

1.5 The importance of nectar composition

Nectar rewards are the most important factor in the foraging activities of bumblebees (see Section 1.9 for additional flower choice criteria). Volume and concentration are the critical parameters for nectar, while the combination and proportions of specific nectar sugars may also influence its nutritive value (Wykes 1952). Temperature, the proximity of competing forage plants and competition from other foragers will all affect foraging patterns through altering the balance between the concentration and volume (and hence attractiveness to bees) of floral nectar (Wratt 1968).

The energetic reward provided by nectar to the foraging bee depends on its volume, its concentration, the volume and depth of the nectar receptacle, and the length of the bee's proboscis. In flowers with tubular corollas such as *V. faba*, the nectar must exceed a certain threshold height in the corolla tube to be within reach of the proboscis. A study of flower choice in red clover demonstrated a significant effect of nectar height in the corolla (Hawkins 1971).

Compared to several other crop plants, e.g. raspberries, field beans produce small amounts of relatively dilute nectar. Free (1993) suggested that "*where possible, field beans should be planted where there are few competing nectar and pollen sources as bees prefer to visit many wild flowers, and Trifolium spp. and Brassica spp. crops to field bean*". Breeding programs designed to improve nectar secretion in a crop could increase insect visitation (Walker et al 1974). In a study of honeybee pollination of soybeans *Glycine max*, the cultivar receiving most insect visits was the one which had the highest percentage of dissolved solids in the nectar, and the largest quantity of

nectar per floret (Erickson 1975). Low levels of early season foraging were explained by low levels of nectar secretion by soybean flowers. Bees tend to forage on those species that give the greatest caloric reward in return for the energy expended in the search for and extraction of the reward (Heinrich & Raven 1972).

If enhanced nectar production can increase the attractiveness of a cultivar to bees, it may have potential for improving crop yield. Work on alfalfa *Medicago sativa* yields has demonstrated a significant relationship between the number of seeds per pod and the average volume of nectar in the flowers (Teuber et al 1983). Greater seed production could be the result of increased bee activity. Alternatively, since the number of seeds in a pod and the nectar volume are both influenced by the vascular supply to the ovaries and nectaries, the cause could be one of simple physiological association.

The average field bean flower secretes on average between 0.4 and 1.6 μl of nectar per day, at a concentration of between 24% and 35% (Stoddard & Bond, 1987). The nectar is held at the base of the corolla tube. Rates of secretion are highest in the early morning and the evening (Free 1993; Stoddard & Bond 1987). In general, the standing crop of nectar within a patch of *V. faba* varies widely over time and space. This variation decreases the ability of the forager to estimate mean reward and to learn which are the most rewarding flower types (Dukas & Real 1993).

1.6 Factors influencing the composition of floral nectar

The causes of temporal and spatial variation in the distribution of the standing crop of nectar can be roughly grouped as pre-secretory and post-secretory in origin, and summarised as follows:

Pre-secretory causes:

- Soil fertility and cultural conditions;
- Differential rates of nectar secretion in different plants;
- Variation in rates of secretion throughout the day and with the progression of the flowering season;

- Influence of atmospheric conditions (including ambient temperature and humidity, precipitation and light intensity) on rates of nectar secretion;

Post-secretory causes:

- Changes in volume and concentration due to equilibration of the nectar with the microclimatic environment (affected by air movement, ambient temperature and humidity and insolation);
- Depletion of nectar by foraging insects and the introduction of foreign substances.

Soil fertility is affected by such various factors as the previous history of the field, levels of husbandry, and the application of fertilisers. Fertilisers may either reduce or enhance secretion, depending on the crop and cultural conditions (Ryle 1954). The fertility and water-holding capacity of the soil are even more crucial in unfavourable climates (Soper 1952). Alfalfa (*Medicago sativa*) clones vary in their attractiveness to honeybees over different conditions of soil structure and richness (Kauffield et al 1969). In excessively moist soil, the sugar concentration of nectar may fall below the threshold for honeybee acceptance. Shuel (1956) found a close relationship between nectar concentration and the concentration of fluids in the vascular system of snapdragons *Antirrhinum majus*. Plant nectaries are real glands with a characteristic active metabolism (Davis et al 1988).

Differential rates of nectar secretion may also be a heritable trait (Walker et al 1974) which can outweigh the effect of soil nutrients (Ryle 1954). Clonal differences in nectar production may be enhanced by "selection" by bees of rewarding flowers, for example in red clover (Hawkins et al 1971) and alfalfa (Teuber et al 1983). Honeybee preference for red clover flowers with greater nectar height has a direct effect on certain components of seed yield, as well as indirectly acting on seed yield through the physiological association of nectar secretion with seed development through the vascular system. Cultivars of various crops including soybean (Erickson 1975) and alfalfa (Walker et al 1974) show significant differences in nectar quality and quantity, which may be mediated by clonal differences in the floral response to environmental conditions.

Nectar secretion in many leguminous crops varies over the diurnal cycle, with the progression of the flowering season, and with variations in atmospheric conditions and the number of daylight hours. Stable temperature regimes produce more nectar in alfalfa flowers than wildly fluctuating temperatures (Walker et al 1974), while warm weather encourages nectar production in soybean (Erickson 1975).

On a finer scale, the microclimate of the flower itself can alter the energetic value of nectar. Nectar may change in volume or concentration as it equilibrates with the microclimate of the nectar receptacle through dilution or evaporation of water, depending on the original volume of nectar, the movement of air over the nectar surface, and the buffering capacity of the floral structure (Corbet, Unwin & Prys-Jones 1979). Open flowers such as raspberry and hawthorn *Crataegus* spp. may secrete copious nectar from which water rapidly evaporates. Crystalline or highly viscous nectar is of little or no value to foraging bees as it cannot be imbibed. Flowers with deep corollas (of which many are zygomorphic, for example *Echium vulgare* and *V. faba*) may secrete less copious nectar which is protected against fluctuations in temperature, humidity and air movement by the microclimatic buffer formed by the corolla. Nectar depletion by insect visitors affects nectar volume and concentration (Corbet et al 1979). Visiting insects may introduce foreign substances into the nectar, such as amino acids (Willmer 1980).

The accessibility of nectar to flower-visiting insects is determined by the distance between the mouth of the corolla tube and the nectar surface. Different cultivars of the same crop legume may exhibit variations in floral structure affecting the accessibility of nectar. Honeybees select flowers of English Single Cut Red Clover on the basis of nectar height in the corolla tubes, but they are rarely attracted to Broad Red Clover because they cannot extract nectar from the longer corolla (Hawkins 1971). The diameter of the corolla influences nectar height but does not influence average nectar volume production (Teuber et al 1983 for alfalfa). Flowers with longer corollas tend to contain more nectar sugar than flowers with smaller corollas. This phenomenon applies both inter- and intraspecifically. The close association between corolla depth and the amount of sugar contained in a flower may be due, at least within a species, to the physiological association of floral development and nectar secretion with the plant vascular system.

1.7 The significance of extrafloral nectaries

Vicia faba is one of many species of flowers which have more than one mode of nectar secretion. The ultrastructure of both the floral and extrafloral nectaries has been studied in detail with the electron microscope (Davis, Peterson & Shuel 1988). Extrafloral nectaries are found on the stipules subtending most of the leaves, and they are demarcated by a dark spot which may function as a nectar guide. The purpose of stipular nectaries is uncertain: Stoddard & Bond (1987) suggest that they serve to maintain the bees' interest in the crop before the secretion of floral nectar.

Stipular nectar is secreted at lower volumes than floral nectar, and is slightly less concentrated. This is because stipular nectaries are supplied by both phloem and xylem vessels, while the floral nectaries are supplied only by the phloem (Davis, Peterson & Shuel 1988). There is no definitive study of the sugar composition of *V. faba* nectar. One analysis of floral nectar using paper partition chromatography found roughly equal proportions of fructose, glucose and sucrose, the combination that is most attractive to honeybees (Wykes 1952). A more recent study found that the floral nectar contained only sucrose, while stipular nectar was composed predominantly of a solution of glucose and sucrose with only a trace of fructose (Davis et al 1988). If selective visits by nectar gathering bees to various plants (or parts of a plant) are influenced by the individual sugars present in the nectar, then differences between the sugar composition of floral and stipular nectar may be of some importance.

At any one time, a large proportion of honeybees foraging on field bean crops in the UK are visiting extrafloral nectaries or obtaining nectar through corolla piercings. In some studies, honeybees making positive visits have been observed to constitute as little as 18-25 per cent of the honeybee population (Free 1962, Bond & Hawkins 1967). In a Danish study (Poulsen 1973), however, honeybees foraging on stipular nectar made up only a very small proportion of total honeybee foragers. Because honeybees may be preoccupied with extrafloral nectaries, colonies should not be moved to crops prior to flowering (Free 1993).

1.8 Nectar robbing in field beans

B. terrestris and *B. lucorum* are the most common nectar robbers in the UK (Free 1993). Honeybees tend to use the holes made by robber bumblebees, but they may also act as primary robbers. Field bean flowers are often impenetrable to honeybee mandibles, but some honeybee colonies have stronger mandibles than others, and some field bean plants and cultivars may be tougher and more difficult to penetrate (Free 1993). Corolla-piercing by bumblebees is less common in the warmer parts of Western Europe and the Mediterranean (Free 1993). Bumblebees are primarily an alpine and North Temperate Zone group, less abundant in warmer regions (Alford 1975; Williams 1986; Prys-Jones & Corbet 1991). In warmer countries honeybees make relatively more positive visits to bean flowers. The numbers of robbed flowers in a field bean crop may be very high. In one study in New Zealand the majority of flowers produced during the early flowering season of the autumn-sown cultivar Maris Bead were robbed (Newton & Hill 1983).

Robbing does not damage the reproductive structures of flowers, nor does it prejudice the mechanics of pollination or pod development (Newton & Hill 1983; Wijibrandi et al 1984). On some occasions negative visits may encourage pollination indirectly by shaking pollen from the anthers onto the stigmas (Free 1993). Flowers that receive visits from long-tongued bumblebees *and* robbers set slightly more seed than flowers visited by long-tongued bumblebees alone (see Table 1.1). Robbed flowers set more seed than unvisited flowers on the first three flowering nodes (Smith et al 1974).

Where short-tongued species are the most prominent members of the bumblebee community the pollinating value of the bumblebee population may be low. In one study (Poulsen 1973) only 21% of 125 bumblebees made positive, pollinating flower visits, whereas 58% of 1110 honeybees made positive visits. In both years of this study *B. terrestris* was the most common bumblebee, making 227 visits in the 1970 study period compared to 8 visits by *B. hortorum* in the same year. Nectar-robbing bumblebees may switch to making positive flower visits for pollen as the day progresses. Poulsen's data suggests that a switch from negative to positive visits by *B. terrestris* occurred at around 1700 hours GMT, which may have coincided with a period during which nectar volumes were too low for profitable robbing, or during which anther dehiscence made pollen a more rewarding resource.

Brian (1957) proposed an interesting relationship between bumblebee tongue length and behaviour. The short-tongued *B. lucorum* and *B. terrestris* have more versatile foraging strategies and a greater tendency towards aggression than other *Bombus* species. Brian suggested that different levels of aggression between species may parallel their readiness to bite flowers.

1.9 Differences in the attractiveness of crop cultivars to bees

Flower choice in bees is mediated by the "attractiveness" of the plant to the insect. Floral attractiveness is the outcome of the interaction of one or more floral stimuli with the insect nervous system. Whether it is positive, negative or indifferent depends on the insect's sensitivity to the stimulus (which may be influenced by the individual's genotype, physiological status and developmental status) as well as on the nature and intensity of the stimulus. Teuber et al (1983) hypothesise that "*bee attraction to a plant species is initially a visual response to colour and mass followed by olfactory response at closer range, with reward as the final stimulus*". Free (1970) states that the olfactory response is more important than the visual response. Erickson (1975) lists genetic differences, climate, cultural conditions, the wild bee fauna and competing plant species as important determinants of the attractiveness of any plant to bees.

Agricultural conditions can lead to significant differences in attractiveness of crop cultivars. A densely sown *V. faba* crop produces fewer flowering nodes per plant and slightly fewer flowers on the inflorescences. This effect is even more marked in poor soil (Hodgson & Blackman 1956). As floral display is a major insect attractant to plants (DeGrandi-Hoffman & Collison 1982), bees are more likely to visit crops or parts of crops in which the floral display is not reduced by competition for nutrients or space.

Since nectar is one of the primary objects of foraging by bees, it is likely that the level of nectar production by any crop will have consequences for the yield. Pederson (1953) found positive correlations between nectar production and honeybee visitation, and between bee visitation and seed production in alfalfa. Ryle (1954) found that clonal differences in nectar production between cultivars of red clover were greater

than differences arising from fertiliser treatments. She concluded that since different genotypes respond differently to environmental factors, the optimal quantity of a particular fertiliser may vary with soil type and plant cultivar. In a study of the attractiveness of alfalfa clones to honeybees 45 of 55 cultivars were found to vary in attractiveness over different locations and years (Kauffield et al 1969). Different species of bees may show decided preferences for sugar solutions containing specific proportions of sucrose, glucose and fructose. The proportions of sugars may vary between plants of the same species within a patch, among individual flowers or florets on the same plant, and over time, for example in red clover (Wykes 1952). This will lead to a fluctuating response from foraging bees. At very low nectar concentrations, some sugars may only be present in trace quantities. Sugar concentration itself is a major factor determining the intensity of bee visitation (Pederson 1953).

Six cultivars of birdsfoot trefoil *Lotus corniculatus* showed almost identical nectar characteristics and secretion patterns, but still differed in their attractiveness to honeybees (DeGrandi-Hoffmann & Collison 1982). The basis of preference was floral display, since the largest numbers of foragers were attracted to those cultivars that produced the most florets. Foraging levels were related to the magnitude of the display, so that honeybee activity on *L. corniculatus* was highest at peak flowering. This supports the hypothesis that foraging is directed towards maximising the ratio of caloric reward to the energetic cost of foraging (Heinrich 1979). Clonal differences in the intensity of the floral display may have a genetic basis or may be a consequence of the cultivar's response to the environment.

The use of artificial flowers to study flower choice in bumblebees suggest that flower colour is a primary signal, but that scent is preferred to colour as a distinguishing feature, and that flower size is unimportant (Free 1970). The attractiveness of a flower to bumblebees may be increased by the presence of nectar guides, which are often associated with contrasting scents. *V. faba* flowers usually have nectar guides, although some white-flowered cultivars (for example Glacier, Toret and Caspar) do not. Flower colour and plant height were found to affect the behaviour of honeybees pollinating Brussels sprouts *Brassica spp.* (Faulkner 1976).

The attractiveness of a small number of highly preferred alfalfa clones to honeybees remained stable over locations and years (Kauffield et al 1969) indicating that some clones have a powerful and persistent attraction, probably with a genetic base. It has been demonstrated that 'olfactory compatibility', i.e. scent, was a significant factor in honeybee preference among 28 alfalfa clones (Loper et al 1974). These authors identified the flower volatiles as a complex of terpenoids, variations in the relative proportions of which led to variations in the 'olfactory quality' of different cultivars to bees. The effect of atmospheric conditions on flower volatiles may vary between cultivars (Erickson 1975, for soybeans). Flower colour, nectar quality and concentration, and pollen availability are also important attractants for alfalfa pollinators.

The yield response of field bean cultivars to insect pollination depends on the balance of heterozygosity and homozygosity in the genotype. The reduction of the yield that may take place in the absence of bees (alternatively, the potential degree of yield improvement with maximal pollination) is variable and dependent on the season and the cultivar (Stoddard & Bond 1987). Since the attractiveness of a cultivar can influence foraging by bees, and since honeybees and bumblebees tend to work within cultivars, for example as in Brussels sprouts (Faulkner 1976), it may be possible to increase crop yield through the activity of bees on some cultivars. This may not apply to all cultivars, because of clonal variations in the plant response to insect pollination (Erickson 1975 for soybeans; Stoddard & Bond 1987 for field beans). Bee preference is an important consideration in the development of new alfalfa clones (Loper et al 1974), and it may be worthwhile to include "attractiveness" as a criterion in future breeding programmes for commercial *V. faba* cultivars.

Stoddard (1986) asserts that "*When contrasting types* [of *V. faba*] *are grown together, the percentage of flowers pollinated by bee activity is constant regardless of floral colour, plant density, plant morphology, or even floral size*". However, Free (1993) suggests that to produce vigorous *V. faba* hybrids, seeds of two lines should be mixed at random during sowing to reduce the effect of differences in colour and scent. This implies that bees do distinguish between field bean cultivars on the basis of colour and scent. The scent of *V. faba* is strong, carries far and is highly attractive to bumblebees (Stoddard & Bond 1987) therefore differences in scent may be important. Stoddard's assertion invites further scrutiny.

1.10 The significance of flowering period

For maximal pollination the field bean crop should flower during the nest provisioning period of social bees. The timing of the development of different castes within the colony cycle can shift from year to year. The work of Chambers (1946) on the variability of flight periods among orchard pollinators illustrated the dependence of pollinator life cycles upon seasonal variables, and how seasonal factors determine the species composition of the community of pollinators on a crop. In 1941 the solitary bee *Andrena varians* was active throughout the month of May, and coincided with the flowering period of apple trees. In 1945, however, *A. varians* became active one month early, and failed to coincide with the flowering of apple that year.

The pollination, fertilisation and yield of a field bean crop depend ultimately on the time of year when the flowers are open (Stoddard 1986b), which depends in turn on the date of sowing and climatic variables. Stoddard & Bond (1987) mention the discrepancy in average yield between winter beans (which flower early in the year) and spring beans. As few as 17% of flowers may be fertilised in crops of autumn-sown winter beans in Northwest Europe. Spring-sown bean crops flower at a time of increased pollinator activity, and of temperatures more favourable to plant growth, floral development, and the growth of pollen tubes.

Pollinator activity often undergoes significant changes during a single flowering season. For crops of broad beans *V. faba major*, clover *Trifolium alexandrinum*, cotton *Gossypium* spp., and citrus in the Giza region of Egypt, Wafa & Ibrahim (1959) found that communities of pollinating insects were largest and richest at the climax of the flowering period for each crop. Heinrich (1976) observed spatial and temporal variation in bumblebee forager spectra on native flower species in Maine. The relative abundance of four bumblebee species foraging on jewelweed *Impatiens biflora* changed greatly throughout the 1972 flowering season (9-23 August) and differed further in 1974. Large changes in forager spectra over a relatively short flowering season may reflect differences between species in the timing of colony life cycles and the development of worker broods, or variation in the preference of a species for *V. faba* depending on which other crops are in flower.

The differences in dates and duration of flowering in cultivars of several crop species have a genetic basis. Scirocco and Sudanese Triple White are early-flowering field bean cultivars, while Punch and Bourdon start flowering when the early varieties have finished. Variation in flowering date within and between cultivars of the runner bean *Phaseolus coccineus* influences the percentage seed set (Williams & Free 1975).

1.11 Environmental determinants of bumblebee activity patterns

Ambient temperature, ambient relative humidity, levels of insolation and air movement are recognised as the most important parameters determining the activity patterns of bees. Prys-Jones & Corbet (1991) provide an overview of the activity patterns of British species of bumblebees. Seasonal temperatures affect the timing of bumblebee colony cycles and may be important in defining the limits of a species' range (Williams 1986).

Bees of the family Apidae are facultative heterotherms, possessing the capacity for physiological as well as behavioural thermoregulation. Bumblebees have more pronounced thermoregulatory abilities than honeybees, and share common physiological mechanisms which have undergone intensive study. The physiology of flight and thermoregulation are fairly well understood (Heinrich 1979; Corbet et al 1993). Facultatively endothermic bees are able to raise their body temperature by shivering the thoracic flight muscles: this procedure is known as 'warm-up'. Bumblebees are able to initiate warm-up at lower ambient temperatures than honeybees, so that they have a wider thermal window for foraging activity. Ambient temperature is critical in determining the point at which foraging may begin, as bumblebees will only forage in very low ambient temperatures if the quality of the resource is sufficiently high. Different climatic factors may influence foraging in different ways. For example, nectar-robbing is less temperature-dependent than pollen gathering in *B. terrestris* on red clover in New Zealand (Wratt 1968).

Under certain conditions bumblebees may show a bimodal activity pattern which peaks in the morning and evening and drops in the middle part of the day due to the danger of overheating and/or in response to increased competition from honeybees (Prys-Jones & Corbet 1991). Bumblebees are large, dark-coloured, well-insulated,

highly active and thus capable of reaching high thoracic temperatures. Overheating is avoided by means of behavioural temperature regulation (such as resting in shade, or evaporating the moisture from a drop of nectar extruded from the crop) or by physiological changes, such as the redirection of blood-flow from the thorax, containing the highly active flight muscle, towards the abdomen (Heinrich 1979).

As well as by shivering the flight muscles, bumblebees are able to raise their body temperature without warm-up, by means of the substrate cycle enzymes fructose diphosphatase (FDPase) and phosphofructokinase (PFKase) in the flight muscle. Substrate cycling maintains thoracic temperatures in non-flying bumblebees and bears an inverse relation to ambient temperature (Clark et al 1976). Non-shivering thermogenesis is energetically cheap compared to standard shivering endothermy, and may even be the most important mechanism for endothermy in bumblebees (Prys-Jones 1986).

Temperature may affect bumblebee activity patterns indirectly, through the nectar secretion patterns of flowers, making them more or less attractive as energy sources. An understanding of foraging patterns therefore needs to consider the influence of temperature, humidity and insolation on nectar characteristics, patterns of nectar secretion, and the attractiveness of flowers through the release of flower volatiles, as well as the direct influences of climate and microclimate on bee activity. Ambient conditions may also affect bumblebee activity through competitive interactions with other organisms: for example the number of *B. ruderatus* foraging for pollen on red clover and lucerne in New Zealand decreases as ambient temperature rises because of increasing competition from honeybees (Wratt 1968).

The indirect effects of environmental factors on nectar availability may explain why Poulsen (1973), studying bees on field beans in Denmark, obtained lower foraging rates from his study than those obtained by Free (1962) on the same crop in southern England. Poulsen attributed this difference to the lower temperatures prevailing in Denmark, but Free (1968) found that honeybees and bumblebees, once active, work at fairly constant speeds regardless of the direct effects of temperature. Heinrich (1979) stated that "*in order to forage optimally, bees must make physiological adjustments that affect foraging rate and energy expenditure*".

Because of the energy expenditure and loss of body fluids inevitably consequent upon active flight, bumblebees must ingest sufficient water during the day to replenish their body fluids. Ambient temperature, relative humidity and air movement all influence how much moisture is lost, while the concentration and volume of nectar determine how much water can be regained. Unlike honeybees, bumblebees do not drink and must obtain all fluids from nectar. If the sugar concentration of nectar is very low, as after a fall of rain, it may contain insufficient sugar to meet their metabolic needs (Kauffield et al 1969). On still, hot days, ambient relative humidity may be very low and nectar may become highly concentrated. Viscous or crystalline nectar does not provide sufficient moisture in hot, dry weather conditions, and it is mechanically impossible for a bee to extract it. The increasing viscosity of nectar may contribute to the decrease in bumblebee activity sometimes observed during the middle of the day. Willmer (1982) provides detailed discussion of the importance of insect water balance in diurnal activity patterns.

Interspecific differences in thermogenic abilities and temperature thresholds for activity may account for specific differences in diurnal activity patterns and foraging ecology, particularly between bumblebees and solitary bees (Heinrich 1976). Prys-Jones (1986) hypothesises that, for bumblebees, "*interspecific differences in foraging behaviour may be related to the activity of substrate cycle enzymes*", and that the activity of FDPase and PFKase may be of equal or greater importance than proboscis length differences in resource partitioning among sympatric bumblebee species. Studies of warm-up rates suggest that all British *Bombus* species have similar capacities for standard endothermic shivering (Stone & Willmer 1989). However, there is significant interspecific variation in levels of activity of the substrate cycle enzymes (Newsholme et al 1972). For example, *B. lapidarius* has a higher threshold temperature for activity on flowers than other species (Corbet et al 1993; Bataw & Willmer 1994 unpublished) than other species, and an unusually high level of FDPase in the thoracic flight muscle (see Sections 1.12 and 5.3). Bumblebee distributions are defined by physiological temperature optima (Williams 1986).

The activity patterns of bees are strongly influenced by light intensity (Corbet et al 1993), although some workers consider that the effect is only pronounced at high levels of insolation (Williams 1986). Bumblebees may be less dependent on clear skies for foraging than honeybees because of their greater capacity for endothermic

warm-up and thermoregulation. In one study of honeybees and bumblebees foraging on runner bean, the number of foragers was greatly dependent on the maximum ambient temperature and the number of hours of sunshine (Free 1968). Insolation may act directly on the body temperatures of the bee and/or via the secretion of floral nectar to influence foraging (Free 1960, for honeybees on fruit trees). Measurements of insolation were omitted from the present study.

Despite their endothermic abilities, bumblebee activity levels are subject to short-term changes in weather. Strong winds discourage foraging (Stoddard & Bond 1987; Simon Potts, personal communication), and foraging generally ceases during rain. Honeybees and bumblebees both prefer to forage in sheltered areas (Smith et al 1972). Bumblebees are less temperature dependent than honeybees (Stoddard & Bond 1987), but like them they are ultimately dependent on the climate.

1.12 Bumblebees: important interspecific distinctions

The six bumblebee species referred to in this study are*B. hortorum*, *B. lapidarius*, *B. lucorum*, *B. pascuorum*, *B. pratorum* and *B. terrestris*, all of which are widespread in the UK (Williams 1982).

Phenological, anatomical and behavioural differences between species help to explain regional variations in patterns of relative abundance, and will influence the competitive status of any species on a food source. Since the number of individual bumblebees exploiting a resource is directly related to the supplies available (Heinrich 1976), the relative abundance of different species foraging on a *V. faba* crop will depend on the relative ability of the individuals of each species to exploit *V. faba* under the physical and ecological conditions pertaining at the site. Spatial and temporal resource partitioning permits the coexistence of a number of different species with similar energy requirements. The interspecific differences within *Bombus* that facilitate sympatry are as follows:

- Proboscis length (morphological variation);
- Colony cycle and development (phenological and temporal variation);
- Thermal biology (physiological variation);
- Foraging patterns and strategies (behavioural variation).

Many workers consider proboscis length to be the most important basis of resource partitioning (Heinrich 1976). British bumblebee species vary widely regarding proboscis length. Tongue length depends upon species, caste and individual size, and within a species there may be wide variation in tongue length and other characters along geographic clines (Brian 1957). The length of the tongue influences the speed with which flowers can be handled and determines which flowers are accessible (Holm 1966). Although there is considerable overlap in the spectra of flowers frequented by common species of bumblebee in the UK (Brian 1957; Fussell & Corbet 1992), there is a strong relationship between the average tongue length of a bee species and the average corolla tube length of the flowers visited by members of that species (Brian 1957).

There are conspicuous differences in the timing of the colony cycle among British bumblebees (Prys-Jones & Corbet 1991). Queens of *B. terrestris* and *B. lucorum* are generally the first to emerge in the spring, while *B. pratorum* may be the last species to produce workers. *B. pascuorum* has the longest colony cycle of the common UK species and workers can be seen up until the early autumn, when colonies of *B. hortorum* have disappeared. The range of available forage plants depends on the timing of emergence or eclosion, so that temporal variation in colony cycles is another factor permitting several species to coexist in the same habitat. Heinrich (1976) describes how long-tongued workers of the New World species *B. fervidus* do not eclose until late in the season, by which time the relatively long-tongued queens of the short-tongued bumblebee species have ceased foraging. Because proboscis length within a species is a function of body size, there are highly significant differences in tongue length between queens and workers of the same species. Caste polymorphism allows the colony to exploit flowers of varying depth. The first workers begin foraging one month after the emergent queens, on different floral spectra (Brian 1957).

Physiology may play an important role in bumblebee foraging behaviour. Prys-Jones (1986) hypothesised that species possessing higher activity levels of FDPase and PFKase in the flight musculature will be able to maintain their body temperature for a longer period in the absence of flight, as they will be less reliant upon shivering thermogenesis for temperature regulation. This author collected data relating to the relative use made by the six ubiquitous UK *Bombus* species of single flowers

(requiring brief perching times and periods of flight for inter-flower movement) and massed flowers (which can be reached by crawling), and found a high positive correlation between the activity of the substrate cycle enzymes in a species and the tendency of workers of that species to visit massed flowers. *B. lapidarius*, which has the highest enzyme activity levels, made the most use of massed flowers while *B. hortorum*, which has the lowest potential for non-shivering thermogenesis, tended to specialise on single flowers. There was no apparent significant relationship between the proportions of observations on massed flowers and tongue length, and Prys-Jones argued that the significance of correlations between tongue length and corolla depth amongst sympatric British bumblebees is largely due to the inclusion of the very long-tongued *B. hortorum*.

Long-tongued and short-tongued UK species show significant behavioural differences, some of which can be directly related to differences in proboscis length. *B. hortorum* tends to forage on flowers having corollas too deep for other bees and invariably extends its proboscis upon landing on a flower. Short-tongued bumblebees are unable to reach the nectar in deep flowers and have evolved more versatile foraging methods such as primary and secondary nectar robbing. *B. lucorum* shows a tendency to forage in exposed habitats and is relatively unaffected by the presence of other bumblebees species. It is more flower-constant when collecting pollen than the long-tongued *B. pascuorum* (Free 1970), and may even visit aphids for honeydew (Brian 1957). *B. pascuorum*, by contrast, tends to forage in sheltered habitats and is submissive rather than aggressive in its behaviour towards other species (Brian 1957). Long-tongued bumblebees get most of their pollen incidentally while foraging for nectar. *B. hortorum* obtains pollen exclusively by this route. *B. pascuorum* makes additional efforts to gather pollen, which Free (1968) describes as "*scrabbling over the anthers*". *B. lucorum* and *B. terrestris* employ divergent strategies when foraging for nectar (corolla piercing) or for pollen (positive flower visits) at flowers with long corolla tubes.

Interspecific variations in mean tongue length, behaviour, physiology, colony cycle and caste polymorphism are all important in resource partitioning. Holm (1966) suggests that even small differences in corolla tube depth may greatly affect the relative abundance of bumblebees on closely-related plant species in neighbouring fields, and Morse (1977) suggested that the adjustment between proboscis length and

corolla tube depth may be so fine that the smaller, shorter-tongued individuals of a bumblebee colony visit the smaller, shallower flowers within a patch.

Foraging efficiency is maximal when the proboscis length of a bee corresponds to the corolla tube depth of the flower visited (Ranta & Lundberg 1980). Optimal Foraging Theory states that optimal foraging behaviour maximises the rate of acquisition of energy (Pyke et al 1977). Flower handling time (exclusive of flight time) may be divided into two components: sucking time (ingesting nectar) and mechanical time (inserting and withdrawing the proboscis). Foraging efficiency is greatly affected by the mechanical time required to extract the reward (Gilbert 1981). This may be why long-tongued bumblebees tend to forage on deep flowers. Nectar rewards from shallow flowers may be less rewarding for a long-tongued bee with a greater mechanical time component than those from deep flowers.

Short-tongued bumblebee species tend to be locally and taxonomically more abundant than long-tongued species, due to the fact that most herbaceous wild plants have shallow flowers (Ranta 1982). Long-tongued species are less efficient on shorter corollas than short-tongued species, and vice versa. In natural systems this translates into divergent niche space, such as that occupied by *Bombus appositus* and *B. flavifrons* on *Delphinium barbeyi* and *Aconitum columbianum* (Inouyé 1978). *B. flavifrons* was the more efficient forager on *Aconitum* (4.1 seconds per flower visit compared to 6.1 for *B. appositus*), while *B. appositus* was more efficient on the slightly deeper flowers of *Delphinium* (2.0 seconds per flower visit compared to 2.9 for *B. flavifrons*). Where the two species coexisted, *B. appositus* foraging was restricted to *Delphinium*, and *B. flavifrons* was restricted to *Aconitum*. Where one species was absent, the foraging range of the other had expanded to include both plant species. Inouyé concluded that the constant removal of nectar from *Delphinium* by the longer-tongued *B. appositus* workers significantly reduced the cost:benefit ratio of foraging at *Delphinium* for workers of *B. flavifrons* .

The distribution patterns of British bumblebee species are discussed in detail by Williams (1982 & 1989). Ranta (1982) provides a more general picture of the regional distribution of Northern European bumblebees. If geographic ranges are defined by thermal optima, it would be expected that the "ecological success" or competitive dominance of a species in the community would be more precarious

towards the margins of its range where it may be restricted to a narrower thermal window. Within these limits the structure of a bumblebee community is influenced by the economics of foraging in terms of actual, not potential, rewards (Heinrich 1979).

1.13 A note on *Phacelia*

Phacelia is a large American genus of annuals belonging to the family Hydrophyllaceae (Hutchinson 1973), of which several species including *P. tanacetifolia*, *P. ciliata* and *P. minor* have been cultivated. The flowers are borne in scorpioid inflorescences on sparingly branched stems. The corollas range in depth from 6-9 mm, are rotate to campanulate and blue in colour. *P. tanacetifolia* (see Plate 2) is the most well-known of the species to have become naturalised in the British Isles (Clement & Foster 1994).

P tanacetifolia has been grown in gardens for ornamental purposes, but in more recent years it has been increasingly cultivated on the Continent as a 'cover crop' on set aside land. Cover crops such as *Phacelia* are easy to establish, may be used as green manure to enhance soil fertility for the following crop, and are considered to limit the carryover of pests and diseases in the arable rotation. *Phacelia* is also recognised to be of great value as a food plant for local bee populations.

Introduction, Part II

The rationale and aims of the project

1.14 Overview

The primary aim of the project described in this thesis was to determine whether cultivars of field bean (*Vicia faba*) show different degrees of attractiveness to bumblebees. This was investigated by means of observations which might indicate whether the bumblebee communities on selected horticultural varieties exhibited significant differences in foraging behaviour, and whether any such differences could be understood in terms of variation between field bean cultivars. It was hoped that this might help to elucidate the roles of nectar secretion patterns, floral morphology and plant architecture in determining the floral choices of different species of bumblebees. The project aimed to consider intraspecific variation in field bean nectar profiles and interspecific variation in bumblebee *V. faba* foraging. Work was carried out on twelve commercial cultivars, with an additional study of bumblebee communities on a nearby crop of *Phacelia tanacetifolia* to provide a local point of comparison.

1.15 Studies of field beans

Field beans have been cultivated for at least 4,000 years, and the range of cultivars now available on the market exhibit an extremely wide range of genetic variation. Most commercial varieties are of standard height (see Table 2.1), however, maximum height is ultimately dependent on the fertility of the soil and the prevailing climatic

conditions. Many tall cultivars come into flower relatively late in the season. Phenological differences in flowering may be related to plant architecture via differential growth rates and the time taken for stems to reach maximum height. The leaves may be rounded or narrow, and vary in size and density of spacing on the plant. The "standard" colour for field bean flowers is white with a black or dark brown wingspot. In some cultivars, a convergence of pigmented veins on the wing petal may act as nectar guides. Pure white varieties are popular in commercial agriculture because the unpigmented flowers are genetically linked to low tannin seed levels and higher nutritional quality. Under UV light, field bean flowers show further differentiation through patterns of light reflectance which may be visible to bees. The intensity of the floral display ranges from sparse (e.g. the wild type *V. faba* var. *paucijuga*) to high (e.g. Scirocco). Late cultivars may not begin to flower until the flowering period of early cultivars is completely over. Clonal differences in patterns of nectar secretion are generally not recognised as of importance for commercial cultivars. High levels of homozygosity may be associated with strong floral fragrance. Variations in the quality of scent of different cultivars may be detected by experienced breeders (G. Ramsay, personal communication), but were not investigated in the current work.

The sources of phenotypic variation in field beans are summarised below:

1. *Plant architecture*:
    - •plant height
    - •leaf size
    - •density of foliage
    - •internode distance
2. *Floral characters*:
    - •flower colour and pattern
    - •presence or absence of wingspot
    - •presence or absence of nectar guides
    - •overall colour
    - •flower size:
    - •length from corolla base to tip of standard petal
    - •functional corolla tube depth
    - •width of corolla tube

3. *Floral density*:
    - •number of flowering nodes
    - •number of flowers per node
4. *Flowering period*:
    - •dates
    - •duration
5. *Nectar*:
    - •concentration
    - •volume
    - •patterns of secretion
6. *Scent*:
    - •strength of fragrance
    - •quality of scent

The field bean cultivars selected for the study exhibited a wide range of this variation. The main phenotypic features of each experimental cultivar are listed in Table 2.1.

For the purposes of this study the experimental cultivars were grouped according to plant architecture. This grouping was based on the preliminary reasoning that since the height and foliage density of a plant influence the microclimate immediately surrounding the plant, and since nectar characteristics are significantly affected by with different architectural configurations might show variation in the characteristics of the standing crop of nectar even if there were little or no genetic basis for nectar differences between cultivars. If, for example, variation in nectar production between field bean cultivars was a heritable trait (e.g. Ryle 1954 for *Trifolium pratense*), plant architectural factors might amplify the genetic effect.

Three architectural groups were recognised (see Table 2.1):

- Dwarf cultivars;
- Medium cultivars;
- Tall cultivars (including late-flowering varieties).

Three cultivars were selected for each architectural group, plus three more late-flowering tall cultivars, with the assumption that increased within-group genetic variation might help to balance out the between-group genetic variation relating to traits other than plant architecture. Despite the statistical complexities that would inevitably result, studying a range of cultivars from a diverse genetic background

offered a means of obtaining a more general picture of bumblebee activity on field beans. In addition, it would suggest which varieties were most hardy under the prevailing climatic conditions and therefore suitable for further study projects. It is to be hoped that the number and range of cultivars selected did not provide an obstacle to interpreting relationships between plants and pollinators in a naturally complex floral environment.

Bumblebees visit *V. faba* for nectar and pollen, but at any one time most bumblebees foraging on field beans appear to be gathering nectar. It was hypothesised that any significant clonal variation in nectar characteristics should be reflected in patterns of flower visitation by bees. There is the further possibility that plant architecture might have a direct effect on bumblebee foraging behaviour; for example through microclimatic factors such as humidity and shade. Whatever the case, it was considered appropriate to base this investigation on a study of the nectar characteristics and secretion patterns of each cultivar. The body of information gathered from such a study is known as a nectar profile, and may provide the major element of the energetic background against which patterns of bumblebee foraging behaviour and abundance can be studied.

1.16 Studies of bumblebees

One of the most important sources of variation in field bean cultivars is the timing of the flowering period. Bumblebee communities vary in space and time (Heinrich 1976) due to interspecific differences in distribution and in the timing of the colony cycle (Prys-Jones & Corbet 1991). Like Heinrich's (1976) bumblebee community on native jewelweed *Impatiens biflora* in Maine, the community structure of bumblebees foraging on field beans appeared to undergo continuous change (see Section 3.3iii). Patterns of species abundance were analysed across cultivars in an attempt to discover whether apparent differences in community structure were simply a seasonal effect.

The species composition of bumblebee communities is partly dictated by geographical distribution as well as by seasonal factors. A review of the literature concerning previous studies of field bean pollination suggest that the forager spectra observed during this investigation differ markedly from communities on field beans

in other, more southerly regions of Britain (Stoddard & Bond 1987). Geographical and regional distribution are among the main factors influencing the array of bumblebees native to any one area, the relative sizes of their populations and the relative ability of different species to compete on a given food source (Williams 1982).

The six bumblebee species observed during the field season are widely distributed throughout the United Kingdom, and are known to taxonomists as the 'Mainland Ubiquitous' group. Regional and local differences in the extent and quality of suitable habitats are powerful influences on bumblebee communities on a local scale (Bond & Pope 1974; Williams 1986; Fussell & Corbet 1992; Corbet, Williams & Osborne 1991). Since *B. hortorum* and *B. pascuorum* are the "best" field bean pollinators in the UK (Stoddard & Bond 1987), it might be advantageous to focus field bean agriculture in areas in which these and other species are locally abundant, such as areas of high floral diversity (Williams 1989). Several authors have demonstrated the negative effect of inefficient pollination on commercial yields (Stoddard 1986a; Bond & Pope 1974; Free & Williams 1976), but further work is needed to establish whether variations in native bumblebee communities are important in terms of crop pollination and yield over a wide range of geophysical and agricultural conditions.

The foraging efficiency of a bumblebee on a nectar source bears a significant relation to the length of its proboscis (Heinrich 1976; Ranta & Lundberg 1980). If commercial cultivars show significant differences in floral structure or patterns of nectar secretion, it can be argued that the relative proboscis lengths of different foraging species will affect their relative foraging efficiency on a cultivar. For example, flowers with longer corolla tubes may be less accessible to bees with tongues of intermediate length, while this effect may be lessened if nectar is secreted in large volumes. Interspecific differences in physiology may also influence foraging efficiency on cultivars with differing architectures.

If activity levels of bees on different crop cultivars can be used as an index of preference (e.g. DeGrandi-Hoffman & Collison 1982 for birdsfoot trefoil) it is reasonable to suppose that if bumblebees showed strong or species-specific preferences for certain field bean cultivars, it might be advantageous for agriculturists to select preferred cultivars for planting. This would have the dual benefit of

maximising visitation by the most efficient pollinating species despite competition from alternative crops concurrently in flower, and of encouraging bumblebee populations in the area. This would be of enormous long-term benefit (Corbet, Williams & Osborne 1991).

The potential of genetically engineering crop cultivars for increased attractiveness to bees through improved nectar yields has already been mentioned. A field study demonstrating a relationship between clonal variations in nectar characteristics and patterns of pollinator abundance and behaviour would justify investment in such research. In addition, it might suggest which commercial field bean cultivars are most productive in a particular area given the constraints of soil fertility, climate and the species composition of the local bumblebee community. These arguments would rely on confirmation in terms of actual seed yields and on detailed investigations of causality which are far in advance of this project. It is hoped, however, that the study provides a general overview of patterns of bumblebee foraging behaviour on field beans in Northeast Fife in 1995, and suggest which factors are the major influences on their activity.

1.17 Choice of observational and analytical methods

Simple strategies of observation and non-interference were followed to obtain the data. For this reason, and despite the complexity of the experimental set-up, the statistical methods chosen to analyse the data were as simple and parsimonious as possible. Methods used and the empirical difficulties encountered during the analysis are discussed in Chapter 2.

Extrapolating from the results obtained in this study to actual patterns in commercial crops is a questionable procedure on two main counts. Firstly, the small scale of most experimental studies may not allow an accurate reflection of what is occurring in the large stands of a commercial crop. The second objection derives from the problems associated with comparing insect populations and crop yields from different areas in which soil fertility levels, weather and agricultural traditions vary greatly (Kendall & Smith 1975). I have attempted to bear this in mind while considering the wider implications inherent in any small-scale field study.

Chapter 2

Materials and methods

2.1 Experimental set-up and planting

Twelve cultivars of field bean were chosen for the study. Three were selected from each of the following groups: dwarf (low-growing varieties which reach an average height of approximately 0.8m at peak flowering, e.g. Caspar, Toret), medium (attaining an average of 1.10m at peak flowering, e.g. Victor, Troy), tall (averaging 1.30 at peak flowering, e.g. Frinebo, Gobo) and late-flowering cultivars (e.g. Bourdon, Punch). All average heights refer to experimental growing conditions. Selecting a number of different varieties for each experimental group was expected to minimise genetic variation between groups by maximising variation for such features as flower colour and number, flowering period and vigour. 360 seeds of each of eleven commercial cultivars and of the wild type (*V. faba* var. *paucijuga*, also known as cultivar 172) were kindly donated by Gavin Ramsay of the Scottish Crop Research Institute at Invergowrie. The differentiating features of each cultivar are described in Table 2.1.

The arrangement of the study plot was chosen to fit the main test for an effect of plant architecture on bumblebee foraging behaviour. The plot was divided into twelve subplots, measuring 2.5m by 2.5m, in three rows and four columns (see Appendix, Fig. 2.1). Each subplot was further subdivided into four miniplots, one miniplot being allocated to each of the four groups of experimental cultivars (i.e. dwarf, medium, tall and late). The miniplots of each subplot were arranged so that tall and tall/late cultivars were adjacent on both sides to medium or dwarf cultivars. This pattern was rotated by 90° from one subplot to the next. The four miniplots were separated by a small gap of 20cm. Cultivars were allocated within this arrangement using a sequence of random numbers. Each cultivar was replicated in four rows to test for gradients in soil fertility, composition or moisture in the plot. Each cultivar was represented in at least two of the three columns.

The study was carried out on a plot of land belonging to the University of St. Andrews in the Northeast of the town. The dimensions of the plot were 27.5m (North-South) by 11.6m (East-West). The plot was well sheltered from sea winds by stands of coniferous trees, young fir and flowering currant bushes. In the early morning the plot was shaded by the pine trees to the Northeast but received full sun during the rest of the day. Soil to the seaward side of the plot was dryer than elsewhere bonfires had been made there for several years. Soil in the central area of the plot was coarse and contained much debris, although all of the larger items were removed. The soil was ploughed up with a Rotavator and dug over to create the twelve subplots. The remaining area was planted with other flowering plants attractive to bumblebees, e.g. *Nasturtium*, *Echium*, *Convolvulus* and *Pulmonaria* to maintain the bees' interest in the site when faba bean nectar might be low.

Systemic weedkillers are traditionally applied immediately prior to planting. In the present study all weedkillers and fertilisers were avoided because of the possibility of unforeseen side-effects on the germination, growth patterns and flowering of the beans. Beans were sown 10 cm apart in rows at 20 cm distance, according to the procedure followed by researchers at the Scottish Crop Research Institute, Invergowrie. The ground was prepared using a wooden 'multidibber'. The resulting holes were approximately 10cm deep, and seeds were dropped into the holes by hand, according to the arrangement described in Fig. 2.1. Between 80 and 90 seeds were planted in each miniplot, giving an average total of 360 per subplot.

Cultivar	Category	Actual mean height at peak flowering (cm)	Date of first flowering (dd/mm)	Date of peak flowering (dd/mm)	Foliage density category (1-3)
Bourdon	late	115 +/- 21	07/07	16/07	3
Caspar	dwarf	82 +/- 10	22/06	30/06	3
Frinebo	tall	133 +/- 13	27/06	03/07	2
Glacier	late	143 +/- 9	06/07	15/07	3
Gobo	tall	138 +/- 13	26/06	03/07	2
Maris Bead	tall	123 +/- 11	30/06	12/07	3
Punch	late	138 +/- 13	07/07	15/07	2
Scirocco	medium	102 +/- 8	17/06	25/06	2
Toret	dwarf	87 +/- 12	27/06	07/07	3
Troy	medium	104 +/- 6	26/06	02/07	2
Victor	medium	103 +/- 4	26/06	01/07	1
172 (wild type)	dwarf	65 +/- 3	26/06	04/07	1

Table 2.1 Major distinguishing features of the experimental field bean cultivars
Category: medium = of standard height.
Actual mean height at peak flowering = average height of plants of each cultivar when the floral display of that cultivar was greatest, and is not necessarily the maximum height reached by the plants (n = 12)
Date of first flowering = date at which the majority of plants have at least one node in flower.
Date of peak flowering = date on which each cultivar was visually judged to be in fullest flower.
Foliage density category (visually assessed): 1 = sparse, with smallish leaves; 2 = moderate; 3 = very dense, usually with large, rounded leaves.

Cultivar	Flower colour	First flowering node (mean)	Flowers per node	Floral density (no. flowers per m^3)	FCD (mm)
Bourdon	pinkish with wingspot	12	5.6	223 +/- 32	12.8 +/- 0.7
Caspar	white	9	6	240 +/- 15	14.2 +/- 0.8
Frinebo	white with wingspot	7	8	197 +/- 27	12.2 +/- 0.4
Glacier	white	11	7	380 +/- 20	13.3 +/- 0.6
Gobo	white with wingspot	7-8	5.6	304 +/- 36	12.4 +/- 0.4
Maris Bead	mauve with wingspot	8	7.8	336 +/- 25	11.1 +/- 0.2
Punch	pinkish with wingspot	11	7.8	180 +/- 18	12.3 +/- 0.7
Scirocco	pinkish with wingspot	5	8	342 +/- 21	13.0 +/- 0.5
Toret	white	8	6.7	260 +/- 12	15.2 +/- 0.6
Troy	white with wingspot	7	4.5	111 +/- 15	12.1 +/- 0.4
Victor	white with wingspot	6	6	238 +/- 23	13.1 +/ 0.3
172 (wild type)	white with wingspot	2-3	1.5	80 +/- 7	10.1 +/- 0.1

Table 2.1 (ctd) Major distinguishing features of the field bean cultivars
First flowering node = average first node bearing flowers counting all nodes upwards from the ground (n = 12).
Flowers per node = average number of flowers on each of the lower (early) flowering nodes of the plant (n = 12).
Floral density category = average number of fully opened (but not senescing) flowers per cubic metre of space at peak flowering (n = 12).
FCD = functional corolla tube depth = average depth (mm) from the nectaries at the base of the corolla to the lowermost point of the aperture (see Plate 1).

Planting took place at the end of April. Ideally, in this area of Scotland, faba beans should be planted from seed during March or early April but spring weather during 1995 was very dry and the soil was too hard. All seeds were planted over a period of three days of fairly dry weather. Soil was raked over immediately afterwards. The first rain fell after several days. Shoots were visible approximately two weeks after planting. Throughout May the weather fluctuated between clear and warm days or cold, wet and overcast, and there was no frost. The growth of other wild plants on the plot was curbed by weeding until the beans were tall enough to overshadow the weeds. During dry periods the seedlings were watered from a nearby source.

The *Phacelia* crop was located on a rise to the Northwest of St. Andrews in a large field belonging to Pipelands Farm. It was bordered on one side by a row of mature trees and fully exposed to the sea breezes. During the flowering period the weather was exceptionally hot and dry, with the exception of occasional sea-fogs. The procedures for collecting data did not interfere in any way with the crop.

2.2 Procedures for the collection of data

Data collected during the study period may be divided into five categories:

- Climatic data
- Nectar data
- Plant data
- Foraging rate data
- Species composition and abundance data

2.2i. Recording climatic variables

Climatic data included measurements of ambient temperature and humidity, which exert a strong influence on nectar characteristics and on the behaviour of insects (Corbet et al 1993; Willmer 1982). Climatic data were used as a benchmark whenever it was appropriate to compare or combine datasets from two or more different days.

Temperature readings were taken using fine thermocouples attached to a Portec thermometer. Measurements of relative humidity were obtained using a pre-calibrated hand-held Vaisala HMI 31 probe. Each instrument was allowed to equilibrate for 10 seconds between placement and reading. Readings were taken at hourly intervals throughout each day of the field season in order to build up a climatic profile for each day. The sensors were placed within the miniplots on a level with the topmost flowering nodes of the cultivar (or, for *Phacelia*, on a level with the majority of flower heads) so that the readings should reflect the ambient conditions experienced by bees visiting the flowers. Readings were also taken at the surface of the flowers to obtain estimates of the difference between ambient conditions and the physical microclimate at and immediately surrounding the corolla.

Wind speed and insolation have a strong influence on temperatures on the ground, on the surface of foliage and in the air. These parameters were not included in the climatic data, with the consequence that estimates of ambient temperature and humidity are bound to have an increased error component.

2.2ii Sampling nectar

Nectar data included measurements of nectar volume and concentration at intervals throughout the day to build up a nectar profile. In addition, for field beans only, the position of the flower on the plant (i.e. node) and any corolla piercings were recorded, in case these factors were found to influence the characteristics of nectar.

Faba bean nectar was sampled with 1 μl glass capillary tubes (Camlab, UK) and analysed in the field using a pocket refractometer (Bellingham & Stanley Ltd, UK). Because of the difficulty of inserting the microcapillary into the flower along the path of the bee's proboscis without removing the flower, breaking the microcapillary or damaging the internal tissues of the flower, the microcapillary was inserted into the base of the corolla, at much the same point at which a robber bumblebee would bite. At all times holes made by microcapillaries and holes pierced by bees were distinct: sample holes were small, neat and central, while robber bumblebees made a double crescent-shaped hole to the left or right of the corolla tube, frequently on the upper surface of the corolla, which blackened rapidly at the edges. Honeybee robbers left a small slit near the base of the corolla tube, usually on the lower sides.

The base of the flower was gently squeezed to help transfer the full load of floral nectar into the microcapillary tube. The data therefore represent nectar production rather than the availability of nectar to a foraging bumblebee. This was considered to be an acceptable standard of measurement since the amount "available" to a human sampler is not necessarily equivalent to the amount of nectar "available" to a bee, which is variable depending on the morphology of the bee's mouthparts. After extraction, the length of the nectar column (in units of 0.05 μl) was noted and the sample was transferred as rapidly as possible onto the refractometer surface to minimise changes due to equilibration with the atmosphere. In the early morning, the corolla tube was first dried externally so that the liquid entering the microcapillary would not be diluted by dew.

Only fully open flowers that showed no signs of senescing were sampled for nectar. It was hoped to sample flowers of the same age; open flowers, however, ranged from those in which the petals had just that day unfolded to those that had already been open for three or more days. This range may be considered representative of the range of nectar-bearing flowers available to foraging bees. At each sampling interval, i.e. for a particular cultivar at a specified time (at intervals of one or two hours), flowers were sampled randomly throughout one or two miniplots. Empty flowers were recorded as negative samples, and were considered to be as relevant to the study as positive samples. Nectar sampling aimed to obtain an estimate of the standing crop of nectar throughout the day corresponding to the nectar crop available to bees.

When microcapillary extraction gave 0.05 μl or less, the sample was recorded as a trace. Trace samples were too small to measure nectar concentration because the sample would evaporate and crystallise immediately upon contact with the refractometer surface. On very hot days, small amounts of concentrated nectar in flowers could crystallise or become so viscous that they would not travel up the capillary tube and a negative sample would be obtained. Personal observations suggest that the threshold sugar concentration for significantly increased viscosity or crystallisation of trace volumes of faba bean nectar was around or above 60%. This is in line with Harder's (1986) hypothesis that the sucrose concentration maximising the rate of energy uptake for a bumblebee should lie between 50-65%. It was not possible to determine whether negative readings on such days were due to no nectar or crystalline nectar, and negative readings cannot strictly be interpreted as a lack of

energetic reward for the bee. But since capillary action of the proboscis is an important mechanical component of nectar feeding, small amounts of highly viscous or crystalline nectar are inaccessible to bumblebees (Harder 1986), and may be assumed to offer no reward.

Robbed flowers were also sampled for nectar, as part of the 'random' selection procedure to test for any differences between the standing crop of nectar in robbed and unrobbed flowers and to test for possible relationships between robbing and nectar quality or quantity. However, because of the inevitability of some degree of bias, these data cannot be used to estimate the proportion of robbing that went on in different cultivars or in the crop as a whole.

On any one day an average of two cultivars were sampled for nectar. Sampling was time-consuming and it was considered preferable to obtain detailed records of two or three cultivars on one day rather than less precise records for a larger number. Once the majority of cultivars had come into flower, nectar samples on any one day were taken from two that were at or close to peak flowering stage. This was to ensure nectar profiles collected on any day would reflect plants at a comparable stage of development.

Phacelia nectar can be easily obtained by inserting the microcapillary into the corolla. At least thirty flowers from three inflorescences were randomly sampled at intervals of one or two hours to obtain an estimate of the distribution of the standing crop of nectar, and grouped according to whether they were on emergent (i.e. the flower heads uppermost in the crop) or on sheltered inflorescences (the smaller, lower, shaded flower heads); and according to whether the flowers were newly-opened, mature or beginning to senesce. Sampling was generally confined to mature flowers. Occasional nectar measurements were also taken from newly-opened and senescing flowers. Because of the open structure of the flowers, *Phacelia* nectar may be quite heavily diluted by raindrops or dewdrops in the corolla.

2.2iii Plant structural and floral dimensions

Field bean data incorporated measurements of plant height, floral density and flower size in order to attempt to quantify structural differences between cultivars. A minimum of ten plants were selected at random from each miniplot and an estimate of average plant height for each cultivar was obtained. Counts of numbers of flowering nodes, numbers of flowers and buds were made at the same time, and combined to obtain an estimate of floral density. The date of first flowering and the date of peak flowering (the point at which floral density was greatest) were recorded for each cultivar. The density of the foliage was assessed by eye from a general consideration of leaf size, leaf spacing and internode distance. Leaf sizes were grouped into three ascending categories denoted 1-3. Foliage density was similarly categorised from 1-3 such that category 3 represents the most foliaceous varieties. For plants in the earlier stages of flowering, vertical growth was still in progress and a number of nodes were still hidden in the cluster of leaves and stipules at the growing apex. The number of flowers per inflorescence was determined by dividing counts of numbers of flowers and buds on a plant by the number of flowering nodes, and combining counts from a minimum of ten plants to give an average. Bean plants tend to have one inflorescence per flowering node. The most important index of flower size was considered to be the functional corolla tube depth (FCD). For the purposes of this study, FCD was defined as the depth of the corolla from the base to the point at which the corolla diverges into the standard and wing petals (see Plate 1). The dimension actually experienced by foraging bees will be the functional corolla tube depth to nectar, which the present study does not attempt to quantify. The FCD to nectar is affected by the volume of nectar in the corolla tube, the diameter of the corolla, the extent to which the bee can push its head into the opening of the flower (as bees were observed to do when foraging for faba bean nectar) and is dependent on the strength of the bee and the length of its proboscis and head. It was assumed that measurements of the basic FCD for each cultivar would indicate the existence and nature of any clonal differences in corolla depth. Measurements of corolla tube depth were also obtained for *Phacelia*.

2.2iv Foraging rates and flower visitation rates

Foraging rate data were based on counts of the number of individual flowers of faba beans or *Phacelia* visited by nectar gathering bumblebees of different species over a certain period of time. These measurements were used to obtain estimates of flower visitation rates (in numbers of flowers per minute). Foraging rates on faba beans were studied separately for bees making positive visits to flowers and those engaged in nectar robbing.

For the purposes of this study, the flower visitation rate of a bee is defined as the mean number of flowers visited in one minute. Flower visitation rate was estimated from the mean time taken by one individual bee to visit a known number of individual flowers, and includes the flight component as well as the probing component of foraging time (Harder 1983). Timings began at points convenient to the observer during the bee's foraging trip. On some occasions it was possible to time the bee and count its visits throughout an entire foraging trip within the plot; most data, however, represent just a segment of a foraging trip. One flower visit for field beans was recorded for each occasion on which the bee landed on the standard petal, pressed it down with its weight (or forced the lower petals apart with its front tarsi) and attempted to push its head into the corolla opening. For *Phacelia*, one flower visit was recorded for each time the bee landed on an inflorescence and probed one or more of the florets. Sufficient data were obtained to make estimates of flower visitation rate for positive and negative flower visits to field bean flowers, and for different bee species on *Phacelia*.

For *Phacelia*, the flowers of which have an entirely different architecture to field beans (see Plates 1 & 2), additional records were kept of the number of inflorescences visited during a certain time period. Separate flower heads were only counted as inflorescences when the bee was forced to make a short flight to reach them (a criterion used by Prys-Jones, 1986, to differentiate between floral architectural types). Some flower heads were so close together that the bee simply clambered or walked from one to the next, in which case they were counted as a "single" inflorescence.

2.2v Species composition and abundance

Data reflecting the species composition of the foraging community took the form of counts at regular intervals. Following the methods of previous studies of community structure (e.g. Fussell & Corbet 1992), bees were recorded during timed walks. For the faba bean plot, timed walks lasted exactly 20 minutes at a constant slow pace, and were carried out at hourly intervals. For each observation of a foraging bee a record was made of its species, foraging behaviour (e.g. positive or negative flower visits or visiting extrafloral nectaries) and the cultivar on which it was observed. Each walk involved on average 2 circuits of the plot including diversions into the lateral and longitudinal paths.

Timed walks in the *Phacelia* field also lasted 20 minutes and followed the western margin of the field so as not to cause damage to the crop. Because of the large numbers of bees active on *Phacelia* at any one time, thorough counts and species records were made at regular intervals of three paces. Timed walks on *Phacelia* were carried out at intervals of 1-2 hours. For both field beans and *Phacelia*, only bees that were actively foraging on the crop were counted as 'observations'.

2.3 Analytical Methods

Numeric data was analysed using Minitab (Release 8.2). Standard statistical methods were applied in an attempt to highlight and to define the most apparent trends and relationships within the data. Statistical analysis focused on points which were felt to be of potential relevance during the field observations. Much of the reasoning conceived prior to field observations was discarded afterwards, as the observations themselves had brought to light more pertinent questions.

2.3i Statistical procedures

Simple statistical methods such as analysis of variance and regression were used wherever possible. This was partly due to the volume of the data, and partly to the conviction that biological relationships within ecosystems can be described without the need for complicated diagnostic tools. Before applying any statistical methods,

individual datasets were first displayed graphically or as a table and studied by eye in order to obtain an impression of possible patterns and interactions. For most datasets, for example those concerning nectar volumes and concentrations, foraging rates, floral dimensions and floral densities, a normal distribution function was assumed. For the situations in which a normal population could not be assumed, equivalent nonparametric techniques were applied.

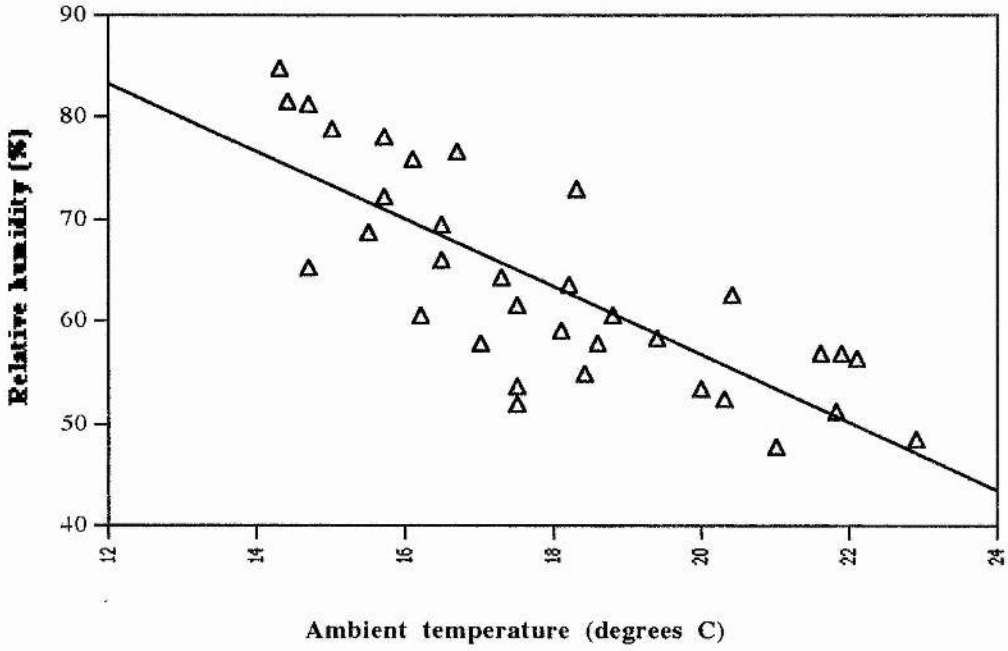
2.3ii Combining datasets

Several different types of data were collected over a number of days, for example nectar data and foraging rate data. In some cases it was necessary to pool individual datasets from different days in order to obtain a larger picture of events, for example the species composition data for the bee community in the field bean plot or on the *Phacelia* crop as a whole, or to search for differences in nectar production between two cultivars which were studied on different days. Since the data were collected over a period of several weeks, during which weather conditions ranged from hot and very dry to cool, overcast and humid, the climatic data for each day were used as a benchmark to compare and combine different datasets. Ambient temperature and ambient relative humidity were strongly and negatively associated ($p = 0.000$, $R^2 = 61.6\%$) across all days of the study (see Fig. 2.2).

2.3iii Problems encountered during the analysis

The main obstacle to the analysis arose from the number of experimental cultivars studied in the plot, and from the fact that for any one factor, multiple options existed. For example, any one of five bumblebee species observed to be foraging on field beans could have been visiting any one of twelve cultivars, and might have displayed one of at least three different types of foraging strategy while visiting flowers for nectar. Not only did ambient temperatures and relative humidities, light intensity and air movement differ from day to day, but there were concurrent changes in flowering stage for the different cultivars on the plot and changes in the community of foragers reflecting seasonal changes in the colony cycle of each species. For some such situations, interpretations have been offered based on a graphical presentation of the data. Another significant problem arose from the non-independence of datapoints. This made it difficult to isolate effects; for example, when studying the effect of

ambient temperature and nectar concentration on numbers of bees. In situations where two or more variables of high potential predictive value were known to be highly correlated, simple graphical methods were used to display the data in relation to each predictor variable.



R.H. = -3.303(Ta) + 122.826

Fig. 2.2 The relationship between ambient temperature (°C) and relative humidity (%) 30/6-28/7/95.

Chapter 3

Results: field beans (*Vicia faba*)

3.1 Field bean nectar profiles

The nectar profile of a field bean cultivar refers to the pattern of change in the quality and rate of secretion of nectar. Mean nectar volume (μl) per flower is here used as an indicator, rather than as a direct measurement, of the rate of secretion.

3.1i The spatial and temporal distribution of the standing crop

Nectar secretion patterns in field beans were observed to vary between cultivars and from day to day within the same cultivar. Fig. 3.1i illustrates the nectar profiles of four cultivars (Scirocco, Caspar, Gobo and Frinebo) on 28/6/95. Despite wide variation within samples there appeared to be an overall pattern of nectar availability in the plot. In general, nectar volume was relatively low in the mornings and began to increase between 11:00 and 14:00 hours. During the afternoon nectar volume underwent a significant drop, and rose again slightly at the end of the day. The variations in this general pattern, illustrated in Fig. 3.1i, suggest unpredictability in the spatial and temporal distributions of the standing crop.

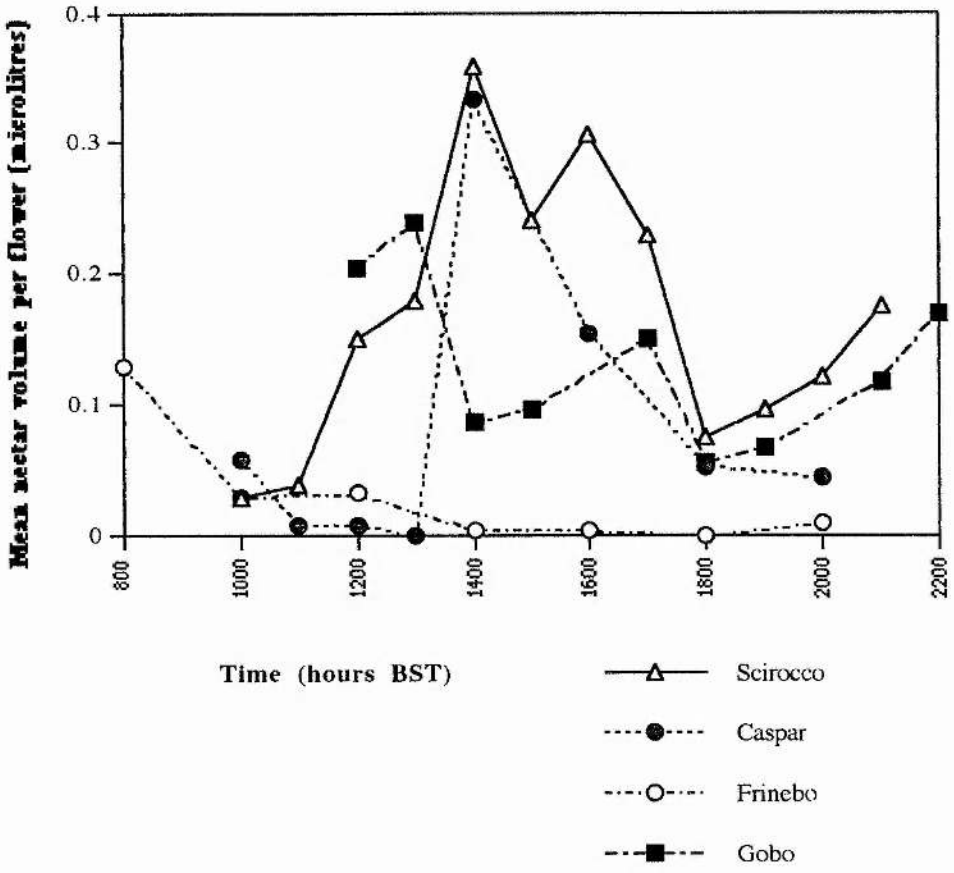


Fig. 3.1i Mean nectar volume (μl) per flower in four cultivars of field bean on 28/6/95.

At any one sampling interval a large proportion of flowers tested for nectar gave negative readings, i.e. contained either no nectar, or nectar too highly concentrated and/or in volumes too small to be detected. On some occasions up to 100% of flowers in a sample of 20 flowers yielded no nectar. Because of the similarities between the movement of nectar through a microcapillary and a bee's proboscis, it may be that these flowers are also relatively unrewarding to the bees. There were significant differences between cultivars in the ratio of positive to negative nectar readings in a sample ($p = 0.000$, $F = 6.69$), the highest frequencies being observed in the early-flowering variety Scirocco. This cultivar is considered to provide a good

illustration of diurnal changes in the proportions of flowers, randomly sampled, which contain at least a trace volume of nectar. The distribution of nectar-yielding flowers (as sampled) in Scirocco on three consecutive days of study is shown in Fig. 3.1ii. The graph shows that nectar rewards were, according to this estimate, most sparsely distributed during the early afternoon between 13:00 and 15:00 hours.

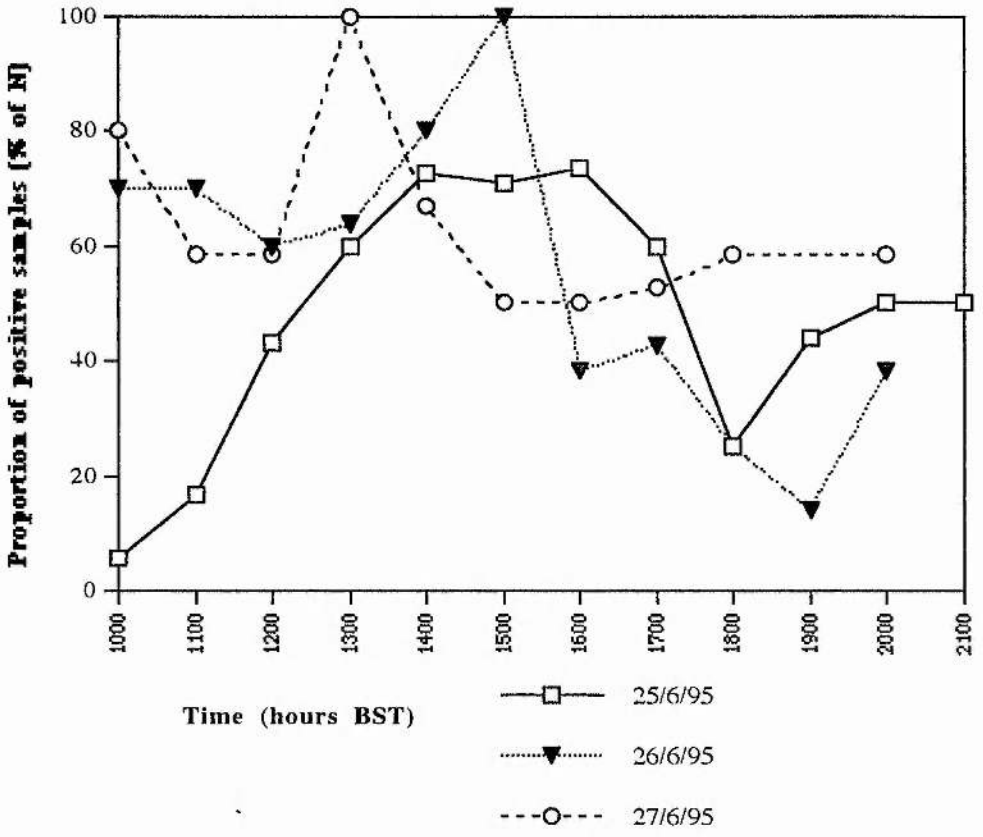


Fig. 3.1ii The distribution of positive nectar samples (the proportion of flowers in each sample which yielded ≥ 0.025 μl (trace) of nectar), in the field bean cultivar Scirocco, 25/6-27/6/95. N (minimum per sampling interval) = 20.

In some cultivars (e.g. the wild type var. *paucijuga*, Maris Bead and Frinebo), the majority of flowers sampled at any one time contained no discernible amount of nectar. Fig. 3.1iii shows the overall proportion of flowers containing at least a trace volume of nectar, as a percentage of all flowers sampled over all days of study (24/6-

15/7/95), in all 12 experimental cultivars. Flowers containing some nectar are considered as "rewarding" flowers in this case.

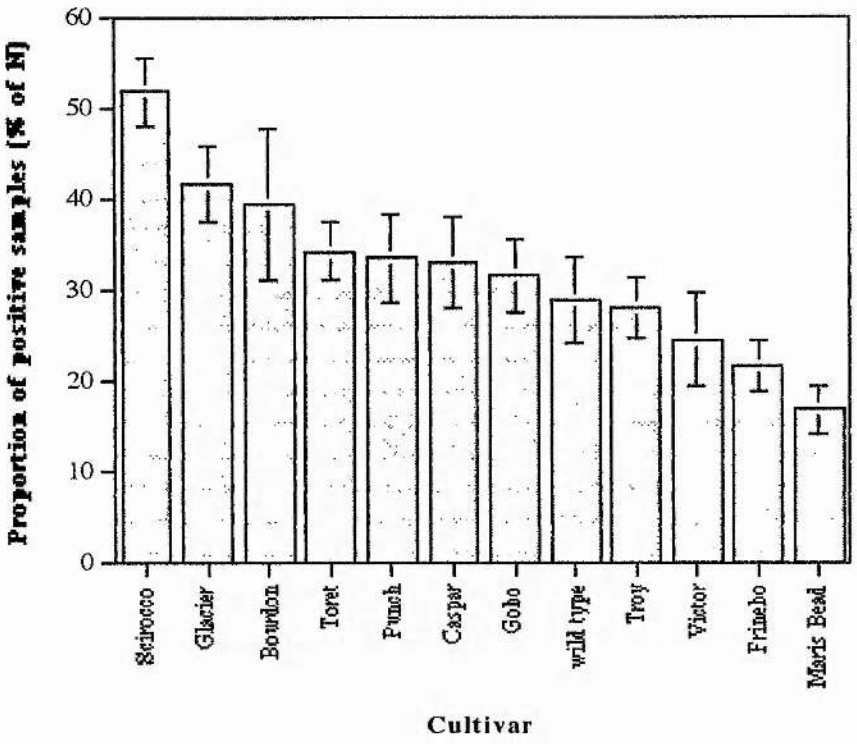
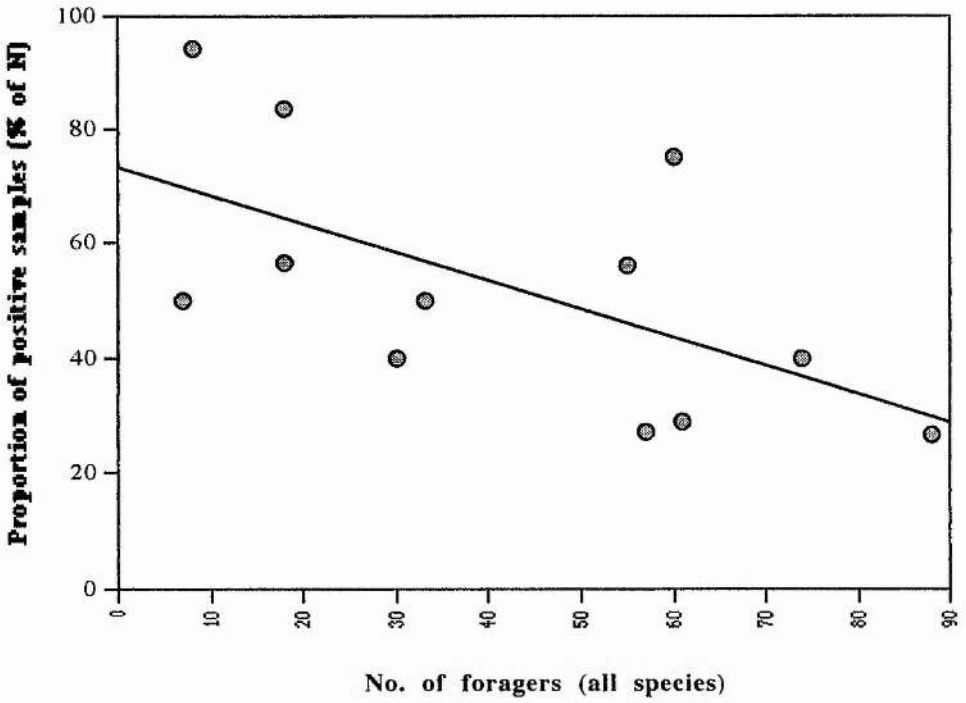


Fig 3.1iii The average frequency of positive nectar readings across all samples for each cultivar, 24/6-15/7/95. N = 3077 (total), N per cultivar ≥ 75.

Ambient temperature and relative humidity were found to have insignificant influences on the ratio of positive to negative nectar readings obtained at any one sampling interval. On 11/7, when numbers of bees on the crop were recorded concurrently with the distribution of nectar, there was a significant negative relationship between the number of foraging bees and the ratio of positive to negative nectar samples, reflecting the depletion of the standing crop by bees (see Fig 3.1iv); $p = 0.038$, $R^2 = 36.3\%$).



% positive samples = -0.496 (no. foragers) + 73.385

Fig. 3.1iv The relationship between the total number of bees (all species) foraging on the crop at any one time and the ratio of positive to negative nectar samples. Data collected from the late-flowering variety Glacier, 11/7/95.

3.1ii Nectar concentration and volume

When all the nectar profiles were combined into one dataset, there was no significant relationship between nectar volume and ambient temperature and relative humidity ($p = 0.567$, $R^2 = 0.5\%$). A graphical representation of this data shows the majority of the datapoints to be clustered between 14-24 °C and between 0-0.25 μl but with no apparent curved or linear trends. However, environmental variables did account for some of the variation in nectar concentration ($p = 0.000$, $R^2 = 34.2$ % for a model including temperature and relative humidity). This relationship is described in Fig. 3.1v. Nectar concentration showed strong and significant positive effects of ambient temperature and humidity when the data were separated for each cultivar: e.g. Toret

($p = 0.000$, $R^2 = 26.1\%$), Frinebo, $p = 0.000$, $R^2 = 30.6\%$), Bourdon ($p = 0.000$, $R^2 = 64.9\%$) and Glacier ($p = 0.000$, $R^2 = 44.4\%$). The effect of ambient conditions on nectar volume for each of these cultivars was not significant. This suggests that the volume of nectar secreted by field bean plants cannot be successfully predicted from environmental variables, and is possibly more directly influenced by some other factor or combination of factors.

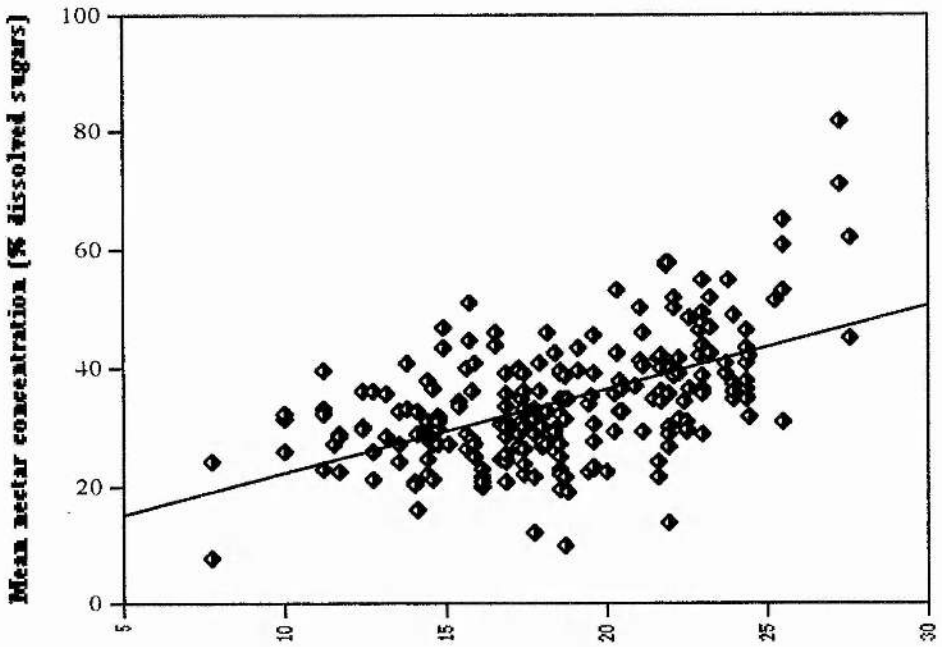


Fig. 3.1v The relationship between *V. faba* nectar concentration (percentage dissolved sugar solids) and ambient temperature (°C) across all experimental cultivars, 25/6-15/7/95. Each datapoint refers to a sampling interval at which N ≥ 20).

Nectar concentration did not bear a simple relationship to nectar volume, as had been expected, either for the combined dataset or for datasets separated by cultivar or by day. The means of these two variables for the combined dataset are expressed in Fig. 3.1vi. The mean volume of nectar in a *V. faba* flower was 0.09 μl, at a concentration of 34.33%.

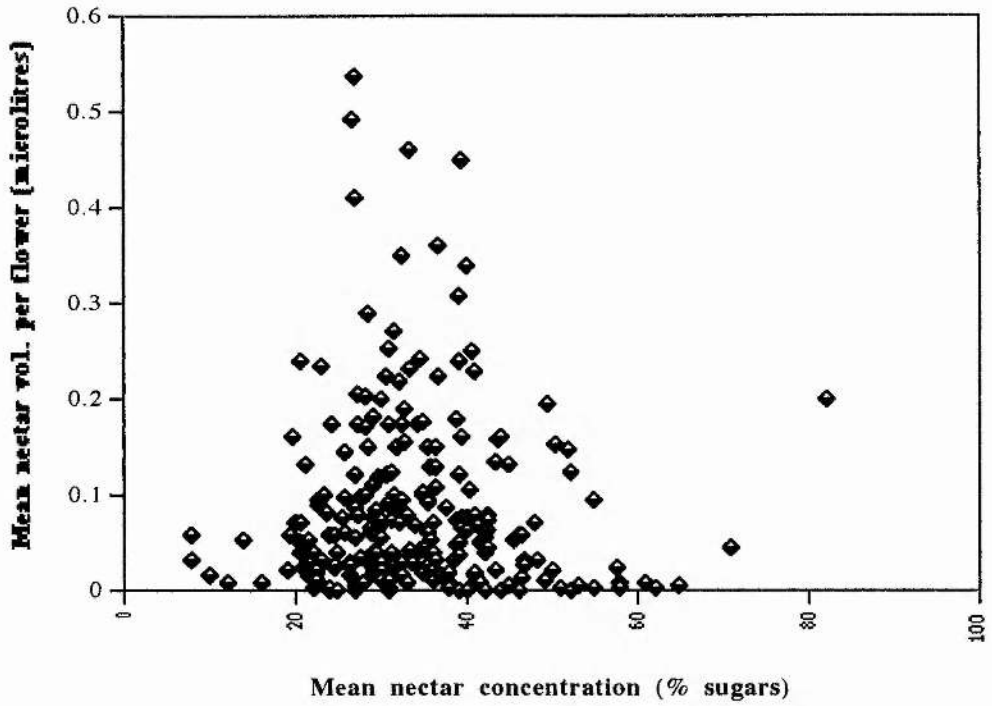


Fig. 3.1vi The relationship between mean nectar volume and mean nectar concentration in *V. faba* flowers 24/6-15/7/95. Each datapoint corresponds to a sampling interval at which N ≥ 20.

Despite the absence of a clear relationship between volume and concentration, nectar volumes throughout the crop were markedly lower on hot, dry days than on humid days. For example, 28/6 was hot and dry with a mean temperature (T_a) of 19 °C 1m above ground, reaching almost 28 °C at 15:00 hours: the average relative humidity (R.H.) was 45%, and bean plants showed signs of wilting. By contrast, 30/6 was cool with mean T_a of 14.6 °C, maximum T_a of only 18 °C (at 15:00 hours) and mean R.H. of 65%. Foraging bees were noticeably more numerous on the latter day. The contrast between the combined nectar profile for all cultivars sampled on each of these two days (Caspar, Gobo and Toret) is illustrated in Figs 3.1vii and 3.1viii.

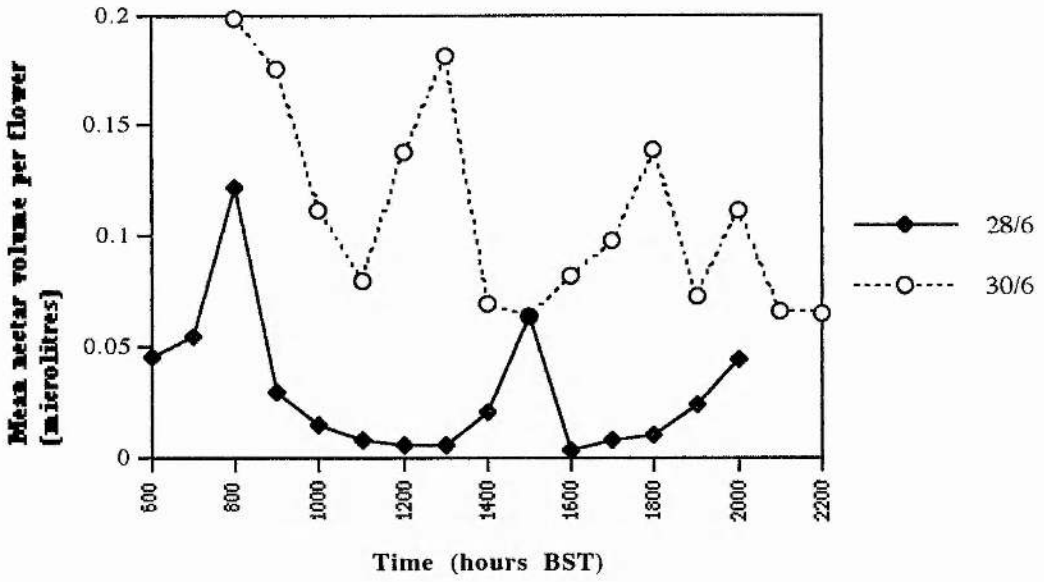


Fig. 3.1vii Mean nectar volume (μl) per field bean flower across all cultivars sampled 28/6 and 30/6/95. N ≥ 40 per sampling interval (1 hour).

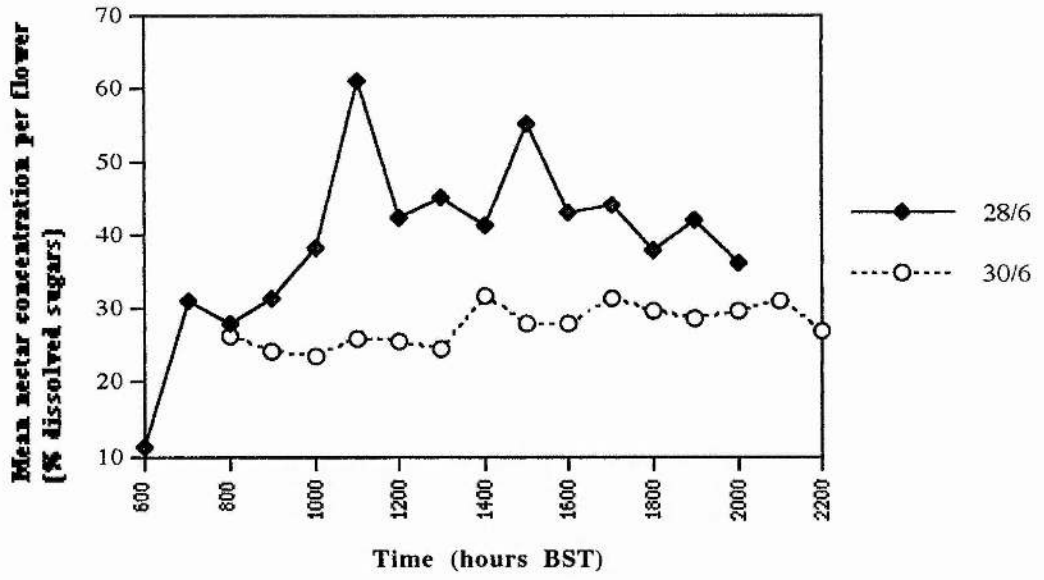


Fig. 3.1viii Mean nectar concentration (% dissolved sugar solids) per field bean flower across all cultivars sampled on 28/6 and 30/6/95. N ≥ 40 per sampling interval (1 hour).

Mean nectar volumes are significantly higher ($p = 0.000$, $F = 30.45$), and mean nectar concentrations significantly lower ($p = 0.001$, $F = 14.03$) on 30/6 than on 28/6/95.

3.1iii Changes in nectar profiles through the flowering season

The quality and quantity of nectar were varied markedly, in some cultivars, with the progression of the flowering season. Some cultivars (e.g. Toret, $p = 0.035$, $F = 2.28$) produced lower volumes of nectar during the first days of flowering compared to later in the season and had slightly more concentrated nectar in the latter days of the flowering period (e.g. Toret, $p = 0.000$, $F = 6.11$). These changes may have been influenced by weather patterns through the flowering season; alternatively, the physiology of nectar secretion may change during growth and senescence of the flowering nodes.

Throughout the study period there was a gradual decrease in the mean nectar volume of flowers sampled from all cultivars ($p = 0.001$, $R^2 = 4.7\%$; Fig. 3.1ix). This bore no relationship to the changes in mean ambient temperature or relative humidity between 24/6 and 15/7/95. Neither did this gradual increase in nectar volume correspond to changes in the ratio of positive to negative nectar samples during the study, which is used as an indicator of the spatial distribution of the standing crop. Nectar concentration showed no trend towards increase or decrease through the flowering season.

The results here presented suggest that nectar concentration may be more directly influenced by environmental variables (ambient temperature and relative humidity) than nectar volume. Changes in the mean nectar volume per flower through the study period may have been due to clonal differences in nectar secretion between cultivars flowering at different points in the field bean flowering season. A further possible explanation is that there may have been a gradual increase in the amount of nectar removed by bees on successive days of the study. Unfortunately the data are insufficient to determine whether there was a progressive increase, over time, in bee activity on the plot.

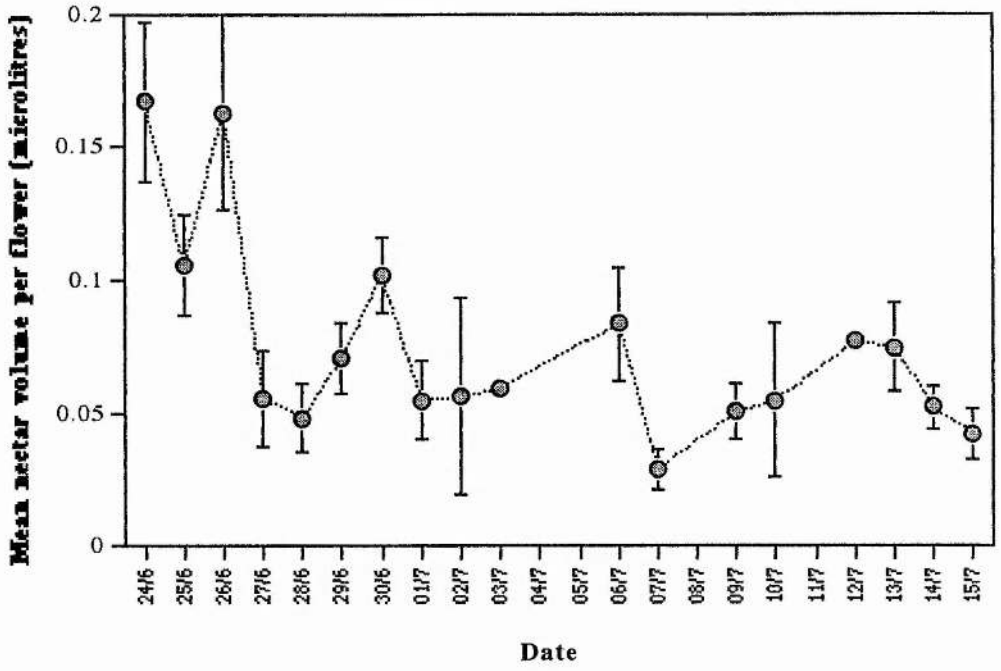


Fig. 3.1ix Changes in mean nectar volume per flower (μl) for *V. faba* (all cultivars) 24/6-15/7/95 (N = 3077).

3.1iv Clonal differences in the characteristics and secretion of floral nectar

The four cultivars studied on 28/6/95 exhibited significant differences in nectar profiles (Fig. 3.1i). The nectar of Scirocco and Caspar was conspicuously more abundant than that of Gobo or Frinebo on this day ($p = 0.000$, $F = 11.37$). When data for all experimental cultivars is combined, clonal differences in nectar become apparent. The differences in mean nectar volume per flower ($p = 0.000$, $F = 9.69$) are more striking than the differences in mean nectar concentration ($p = 0.048$, $F = 1.85$), although both are statistically significant. The data presented in Fig. 3.1x represent nectar profiles from 3-5 separate days for each cultivar and, for each cultivar, cover nectar production across the range of weather conditions encountered during the study.

Fig. 3.1x shows that Scirocco had the most abundant nectar and the wild type (var. *paucijuga*) the least abundant. Maris Bead also had a low mean nectar volume per flower, which may be connected to the fact that, like the wild type, this cultivar has

relatively small flowers. Victor had the highest mean nectar concentration per flower; the wild type had the lowest. The nectar of Glacier and Gobo was also relatively dilute. Nectar of most cultivars, however, appeared to be clustered within the range of 0.05-0.1 μl per flower, at an average concentration of 32.5-37.5%. Fig 3.1iii shows that the frequency of "rewarding" flowers (i.e. yielding at least a trace of nectar when sampled) was highest in Scirocco, Bourdon and Glacier. "Unrewarding" flowers were most frequent in Maris Bead and Frinebo.

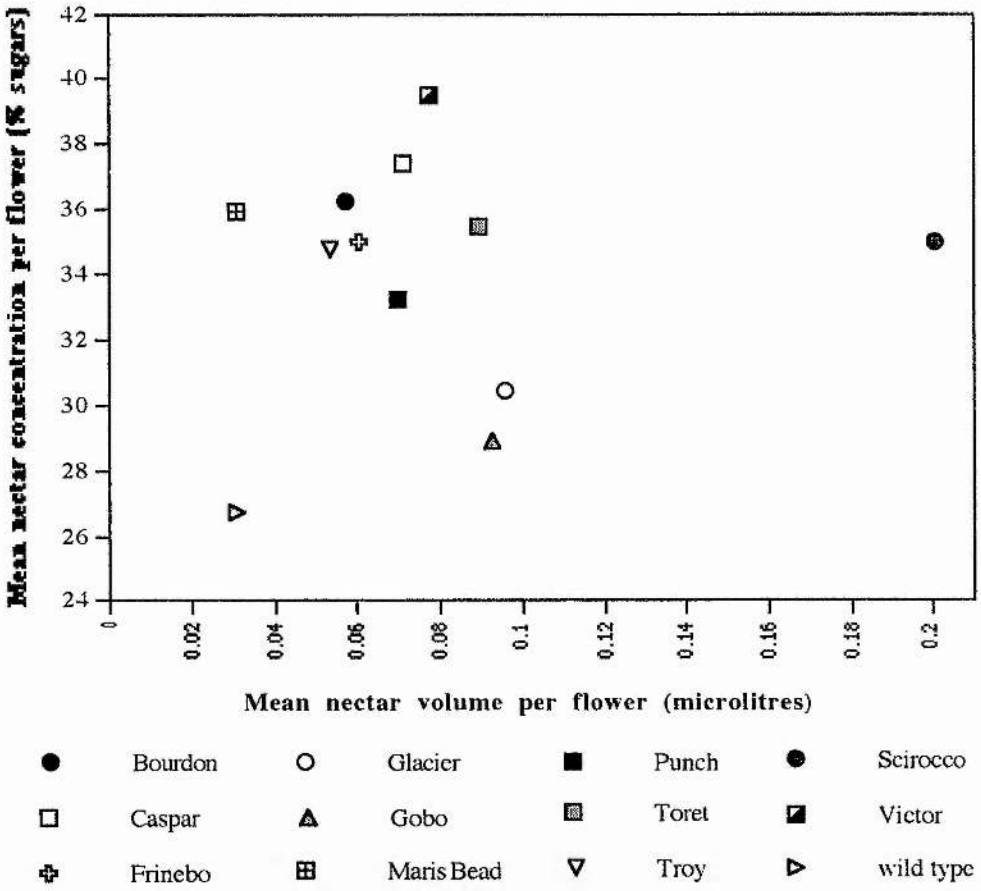


Fig 3.1x Average nectar characteristics of the 12 experimental cultivars: mean nectar volume (μl) and mean nectar concentration (% dissolved sugar solids) per flower. For each cultivar, N ≥ 75.

When the cultivars were grouped according to their traditional height categories (dwarf, up to 90 cm at peak flowering; standard, 91-110 cm at peak flowering; tall,

111 cm or above at peak flowering), there were found to be significant differences in mean nectar volume per flower ($p = 0.000$, $F = 15.1$), but not in mean nectar concentration. Standard cultivars produced slightly higher mean volumes of nectar per flower than either dwarf or tall cultivars (see Table 3.1), suggesting that nectar secretion may be influenced by field bean breeding programmes.

Height category	**Standard**	**Dwarf**	**Tall**
Height range (cm)	91-110	≤ 90	≥ 111
Mean nectar volume per flower (μl)	0.136 +/- 0.016	0.070 +/- 0.009	0.064 +/- 0.006
Mean nectar concentration per flower (% sugars)	35.45 +/- 1.60	34.29 +/- 1.14	33.52 +/- 0.94

Table 3.1i Mean nectar characteristics of field bean cultivars within three height categories (N = 3077).

Foliage density category had no effect on nectar characteristics. White cultivars (e.g. Glacier, Caspar and Toret) tended to have slightly higher volumes of slightly more concentrated nectar than varieties with coloured flowers (see Table 3.1ii), but this effect was not statistically significant. Neither the floral density (number of open flowers per m^3), the date of first flowering, date of peak flowering or the length of the flowering period had significant effects on the quality or quantity of floral nectar.

Flower colour	White	Coloured
Mean nectar volume per flower (μl)	0.085 +/- 0.007	0.075 +/- 0.017
Mean nectar concentration per flower (% sugars)	34.45 +/- 2.09	33.94 +/- 1.29

Table 3.1ii Mean nectar characteristics of field bean cultivars with white vs. coloured flowers (N = 3077).

3.2 The behaviour of bees on flowers, and rates of flower visitation

3.2i Categories of flower visitation behaviour

Bees visiting the field beans exhibited a variety of foraging strategies. Three types of flower visitation behaviour were identified as follows:

1. Positive flower visits took place when the bee alighted on the flower and probed (or attempted to probe) the corolla through the frontal opening for nectar and/or pollen;
2. Negative flower visits, also known as nectar robbing, occurred when a bee attempted to reach the nectar by piercing a hole at the base of the corolla tube, or attempted to remove nectar through a pre-existing hole; and,
3. Visits to extrafloral nectaries, involving the collection of nectar from the stipular nectaries at the base of the uppermost leaf-bearing nodes.

The proportions of each species engaged in each category of flower visitation behaviours on 10/7 and 11/7/95 are listed in Table 3.2i. Fig. 3.2i illustrates the proportions of individuals of all bee species engaged in each behavioural type.

The incidences of the three foraging strategies appeared to change throughout the day. Fig. 3.2i shows that visits to extrafloral nectaries were most frequent in the early

morning, corresponding to the period of lowest bee numbers. *V. vulgaris* was responsible for most visits to extrafloral nectaries. Levels of nectar robbing tend to peak in the late morning and evening, before and after (respectively) peak abundance of "legitimate" foragers. Comparison with data concerning the relative abundance of different species (see Section 3.3), and with field observations, indicates that species composition was the major determinant of the frequencies of different foraging strategies employed by insect visitors to the crop. For example, positive flower visits are by far the most frequent behaviour (between 13:00 and 18:00 hours) when the majority of the foraging community consisted of *B. hortorum*.

Species	Date	N	Behaviour		
			1	2	3
Apis mellifera	10/7	**33**	64%	19%	19%
	11/7	**14**	86%	14%	-
Bombus hortorum	10/7	**368**	100%	-	-
	11/7	**276**	100%	-	-
B. lapidarius	10/7	**84**	100%	-	-
	11/7	**14**	100%	-	-
B. lucorum	10/7	**3**	33%	67%	-
	11/7	**25**	8%	92%	-
B. pascuorum	10/7	**195**	99%	-	1%
	11/7	**155**	99%	-	1%
B. pratorum	10/7	**0**	-	-	-
	11/7	**5**	-	100%	-
B. terrestris	10/7	**1**	-	100%	-
	11/7	**2**	-	100%	-
Vespula vulgaris	10/7	**40**	-	-	100%
	11/7	**35**	-	-	100%
Totals (all species)	10/7	**724**	92%	1%	6%
	11/7	**526**	88%	6%	7%

Table 3.2i Proportions of individuals of eight hymenopteran species engaged in three types of foraging behaviour (10/7-11/7/95). The data are presented as percentages, with the exception of sample sizes (N), in bold type.

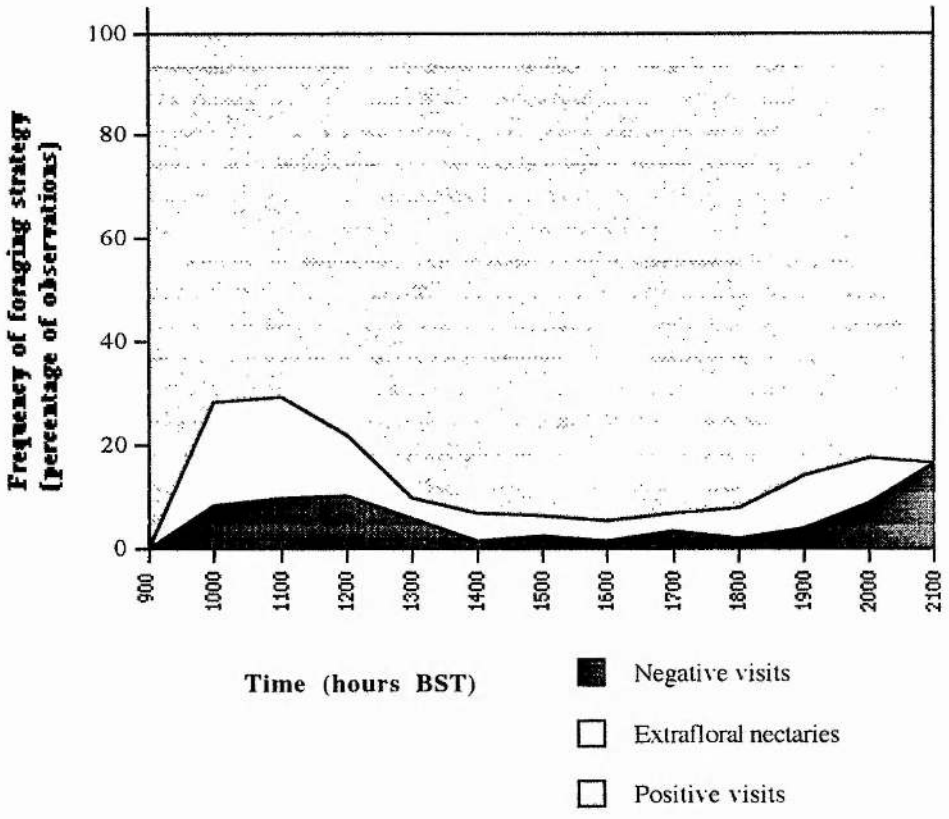


Fig. 3.2i Frequency (percentage of total observations) of the three main types of flower visits for eight hymenopteran species (*A. mellifera*, *B. hortorum*, *B. lapidarius*, *B. lucorum*, *B. pascuorum*, *B. pratorum*, *B. terrestris* and *V. vulgaris*) on field beans (10/7-11/7/95). Sample sizes as in Table 3.2, combined.

a. Positive flower visits

The majority of visits by bees to the bean flowers involved the collection of nectar and/or pollen from the frontal aperture of the corolla. 92% of the total observed flower visits on 10/7 and 87% on 11/7 were positive. *B. hortorum* carried out 55% of these on 10/7 and 60% on 11/7. *B. pascuorum* accounted for 29% on 10/7 and 33% on 11/7. *B. lapidarius* performed 12% of observed positive flower visits on 10/7; however, this species was present only in small numbers on 11/7 and carried out only

3%. *A. mellifera* accounted for 3% of positive visits on 10/7. The relative distribution of species for all positive flower visits observed on these two days are combined in Fig. 3.2ii.

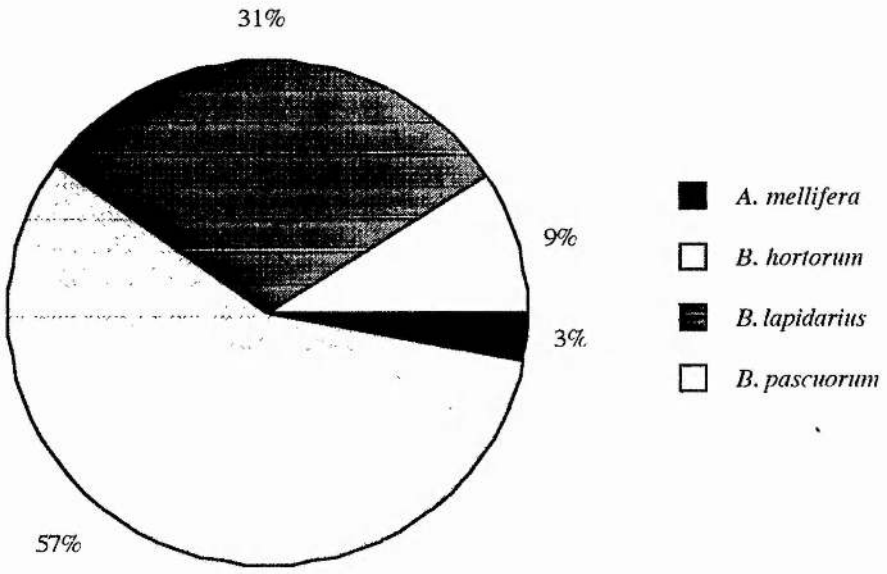


Fig. 3.2ii Bee species responsible for all observed positive flower visits (10/7-11/7/95). Sample size = 1127.

Bumblebees making positive visits to flowers showed specific differences in the nature of their probing. For example, *B. hortorum* and *B. pascuorum* often attempted to enter closed flowers or late buds by forcing the petals open with their heads, whereas *B. lapidarius* was never observed do this.

b. Negative flower visits

Nectar robbing was accomplished by individuals of *B. terrestris*, *B. lucorum* and *A. mellifera*. Robbing (primary and secondary) accounted for only 1% of 724 flower visits on 10/7, and 6% of 526 visits on 11/7, when the weather was markedly cooler and more overcast. Honeybees carried out both types of robbing behaviour, whereas bumblebees (with the exception of *B. pratorum*) acted only as primary robbers. The number of honeybees active on the crop at any one time (and engaged in both positive and negative visits) generally exceeded, by far, the number of robber bumblebees. On 10/7 *A. mellifera* comprised 67% of nectar robbing individuals, *B. lucorum* 22% and

B. terrestris 11%. These proportions on 11/7 were, respectively; 6% (*A. mellifera*), 74% (*B. lucorum*) and 13% (*B. terrestris*), with the addition of three observations of small *B. pratorum* workers acting as secondary robbers and accounting for 6% of all observed negative flower visits on that day. Fig. 3.2iii illustrates the proportions of different species accounting for negative flower visits across these two days.

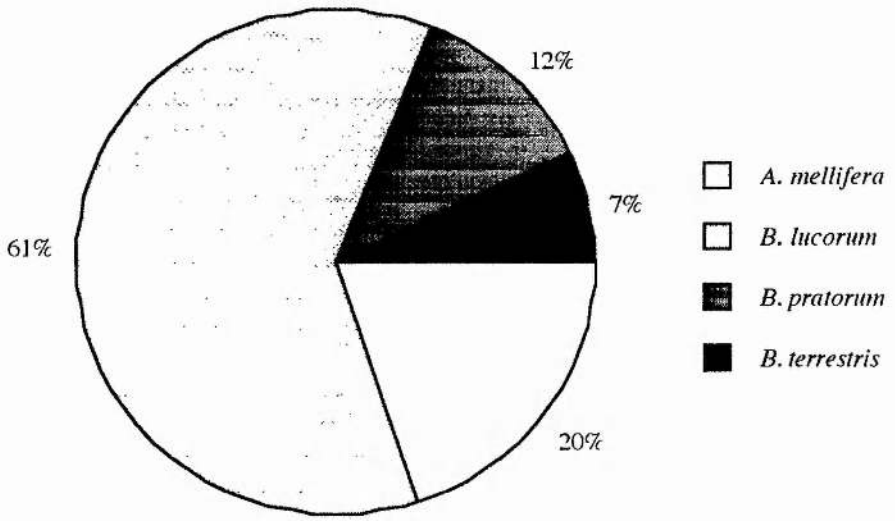


Fig. 3.2iii Bee species responsible for all observed negative flower visits (10/7-11/7/95). Sample size = 40.

Robber bumblebees often performed positive and negative flower visits on the same trip, and even on the same plant. For example, more than one *B. terrestris* queen was observed to probe flowers from the mouth of the corolla and, having found no reward, clambered to the origin of the node and began to bite the corollas (26/6 and 1/7). *B. lucorum* workers mixed positive and negative visits in an apparently haphazard manner at the same node (27/6 to 15/7). A *B. terrestris* queen was seen on one occasion to probe the front of flowers that had previously been robbed (11/7). Robber bumblebees tended to pierce the upper surface of the corolla base, whereas honeybees tended to bite the under surface.

Nectar robbing was most evident in the evening (between 20:00 and 21:00 hours), by which time most bee activity had died down and there was an audible crunch of

mandibles on corollas. Robber bumblebees were often noted for the speed with which they robbed successive flowers at the same node.

c. Visits to extrafloral nectaries

Wasps were frequently observed to collect extrafloral nectar (83% of observed visits to extrafloral nectaries on 10/7, and 95% on 11/7), although they also patrolled the bean leaves in search of aphid and weevil prey. Honeybees carried out 13% of visits to extrafloral nectaries on 10/7, but were not observed to collect stipular nectar on 11/7, when ambient conditions were cool and overcast. Small *B. pascuorum* workers were responsible for 4% of extrafloral visits on 10/7, and 5% on 11/7. The proportions of species visiting extrafloral nectaries over both days are illustrated in Fig. 3.2iv.

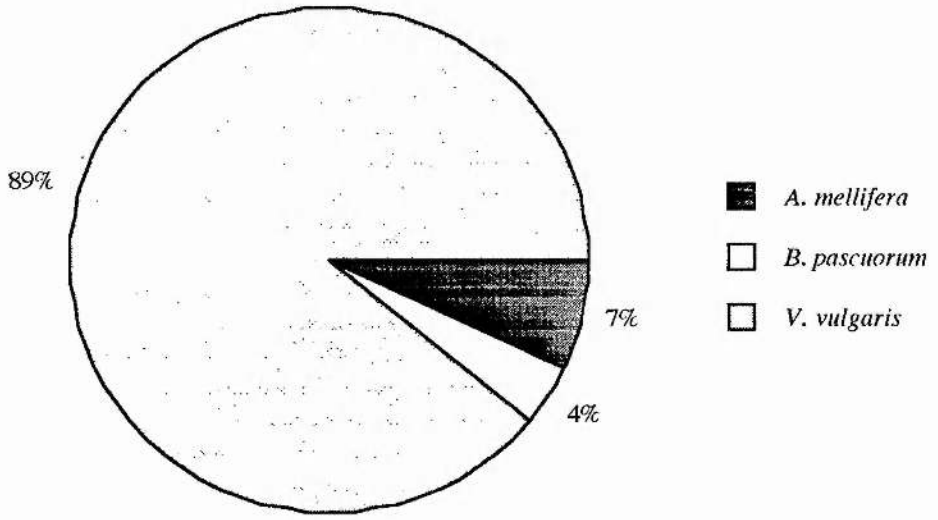


Fig. 3.2iv Hymenopteran species performing all observed visits to stipular nectaries (10/7-11/7/95). Sample size = 83.

A. mellifera often collected stipular nectar in the morning when the bean flowers were still closed, and when there was little other bee activity. Wasps were active on extrafloral nectaries from 06:00 hours. The only bumblebees observed to collect extrafloral nectar were small *B. pascuorum* workers, which were noticed licking the undersurface of the stipules on hot dry days when floral nectar was low in volume and

highly concentrated, and occasionally during the morning prior to the main influx of bumblebee foragers.

3.2iv Flower visitation rates

The rate of flower visitation is here defined as the mean number of individual flowers probed per minute. Estimates were obtained for *B. lapidarius*, *B. hortorum*, *B. pascuorum* and *A. mellifera* making positive flower visits, and for *B. lucorum* and *B. terrestris* making negative visits (see Table 3.2ii). The duration of flower visits, as measured in the field, varied markedly and unpredictably. The data indicate that *B. lapidarius* was the most rapid forager making positive flower visits, closely followed by *B. hortorum*. Flower visitation rates for *B. pascuorum* were generally slower and covered a wider range than those for *B. lapidarius* and *B. hortorum*, but this difference was not statistically significant ($p = 0.504$, $F = 0.69$). Small sample sizes for the latter two species mean that a large error must be associated with the two estimates for nectar robbing.

Species	Type of flower visit	N	Mean time per flower (sec's)	FVR (flowers per minute)
B. lapidarius	Positive	12	6.95 +/- 0.89	9.84 +/- 0.96
B. hortorum	Positive	85	6.98 +/- 0.32	9.82 +/- 0.36
B. pascuorum	Positive	41	9.49 +/- 1.58	9.05 +/- 0.63
A. mellifera	Positive	6	11.5 +/- 2.78	8.10 +/- 2.98
B. lucorum	Negative	3	6.61 +/- 0.64	9.24 +/- 0.83
B. terrestris	Negative	2	14.55 +/- 4.70	4.60 +/- 1.49

Table 3.2ii Mean times per flower and mean flower visitation rates (FVR) of different bee species on field beans (26/6-18/7/95). N = sample size.

Flower visitation rates for the foraging community as a whole, for all bee species making positive flower visits, and for *B. hortorum*, *B. lapidarius* and *B. pascuorum* separately, were tested for an effect of the following factors; ambient temperature, ambient relative humidity, nectar concentration, nectar volume, cultivar, flower size and late-flowering versus early-flowering cultivars. No significant effects were

discernible in any case. Nor did the above factors appear to affect the proportion of positive to negative flower visits. It is concluded that, because of the large number of experimental cultivars, sample sizes were too small to ascertain whether there were any differences between the bee species visiting, or types of flower visits made to, different cultivars over and above the seasonal variation in forager spectra (see Fig. 3.3xv). Focusing the collection of data onto three or four cultivars and obtaining larger samples would also allow investigation of the possibility of differences in foraging rates of the same bee species on different cultivars.

3.3 The size and species composition of the *V. faba* bee community

3.3i The faba bean community

The seven bee species observed on the faba bean plot during the entire study period (24/6-15/7/95) were: *B. hortorum*, *B. pascuorum*, *B. lapidarius*, *A. mellifera*, *B. lucorum*, *B. pratorum* and *B. terrestris*. The relative abundance of species in the bee community was estimated from counts made during timed walks (Fig. 3.3i). All estimates of relative abundance are given in the form of an actual or mean percentage of the total number of bees observed during a timed walk of twenty minutes carried out at hourly intervals between 10:00 and 21:00 hours BST.

Many other insects were frequently observed inhabiting or visiting the field beans. These included: various sawflies (Hymenoptera) and wasps (Hymenoptera, Vespidae), the latter often seen visiting extrafloral nectaries; butterflies and moths (Lepidoptera) which occasionally basked on the bean leaves, and on one occasion a moth was seen to probe a bean flower for nectar; a large number of flies (Diptera) including hoverflies (Diptera, Syrphidae) and a variety of bumblebee mimics; aphids (Hemiptera) and weevils (Coleoptera, Curculionidae) which formed the principal prey of the wasps visiting the plot, and beetles (Coleoptera) from a number of families, including Elateridae observed to take nectar from the stipular nectaries.

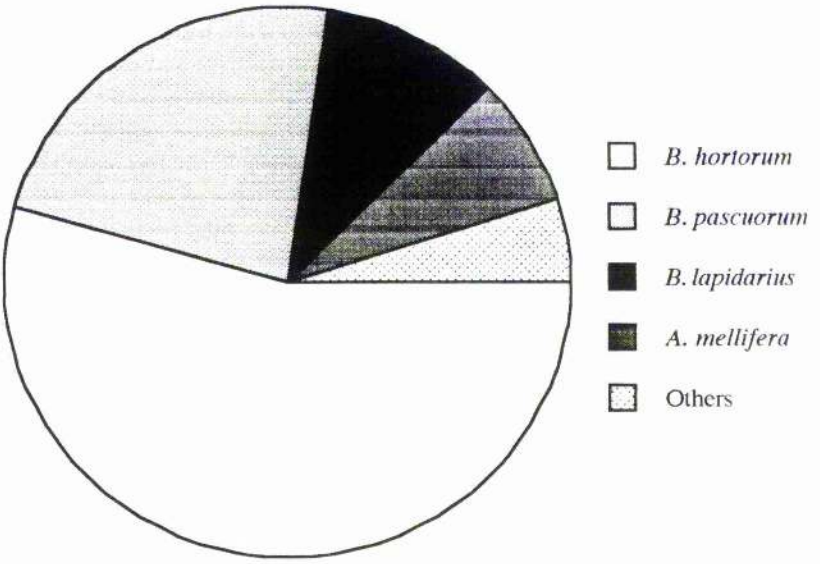


Fig. 3.3i Relative abundance of bee species foraging on field beans (10/7-15/7/95). "Others" comprise *B. lucorum* (4%), *B. terrestris* (0.5%) and *B. pratorum* (0.1%).

Bee species show characteristic activity profiles throughout the day. Bee activity on the bean plot tended to be very low during the morning. After 12:00, numbers of bees began to rise steeply, to reach a peak between 16:00 and 17:00. Most bees observed foraging between 08:00 and 11:00, and between 19:00 and 20:00 were large individuals of *B. hortorum*. *B. hortorum* tended to be the first and last bee to be active in the morning and evening. After 20:00 there was generally very little bee activity on the beans apart from large individuals of *B. hortorum*. *B. hortorum* was the most abundant bee species on the field bean plot on all days from 10/7 to 15/7/95. Typical diurnal changes in the number of bees in the plot are illustrated in Fig. 3.3ii. Typical diurnal changes in the number of individuals of different species are illustrated in Fig. 3.3iii.

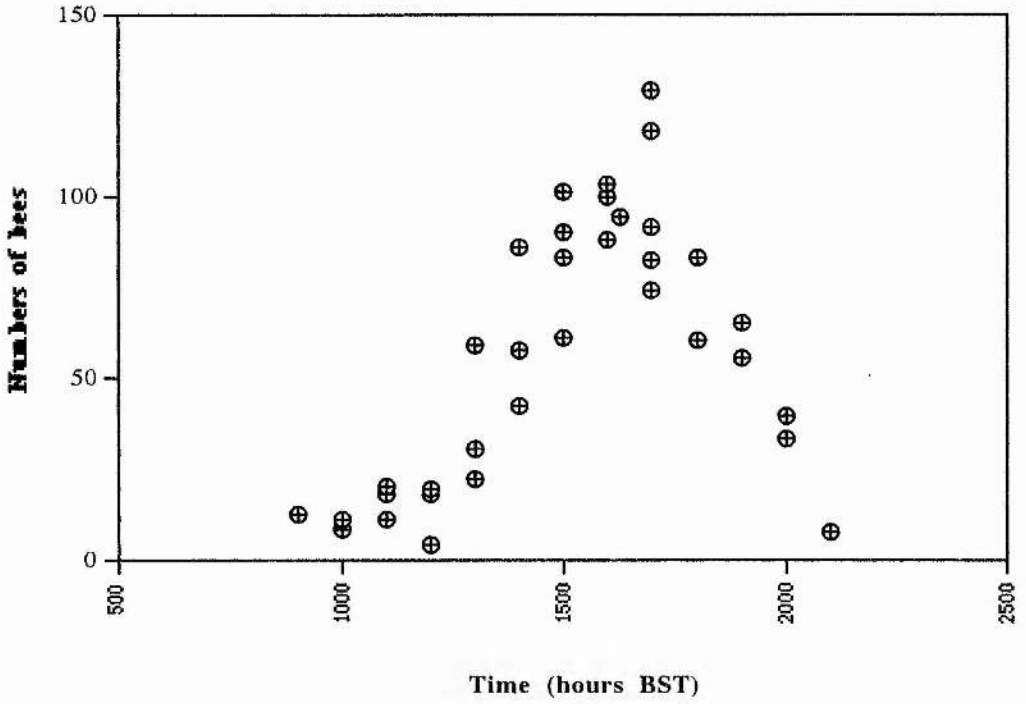


Fig. 3.3ii Changes in the mean numbers of bees (all species) foraging on field beans throughout the day (10/7-15/7/95).

The peak in bee activity at approximately did not correspond strictly to the general changes in ambient temperature. Temperature tended to peak during the middle of the day (12:00 to 15:00) and to fall slightly during the afternoon, although it varied greatly from day to day (temperatures at 16:00 varied from 15-23°C from 1/7 to 15/7/95). No significant effect of temperature could be detected by regression analysis of bee numbers (of all species and of individual species) on temperature across all days of observation, suggesting that bee activity on field beans is not primarily temperature-dependent. Plots of bee activity from 1/7 to 15/7/95 against ambient temperature (°C), however, do suggest a discernible relationship (Fig 3.3iv).

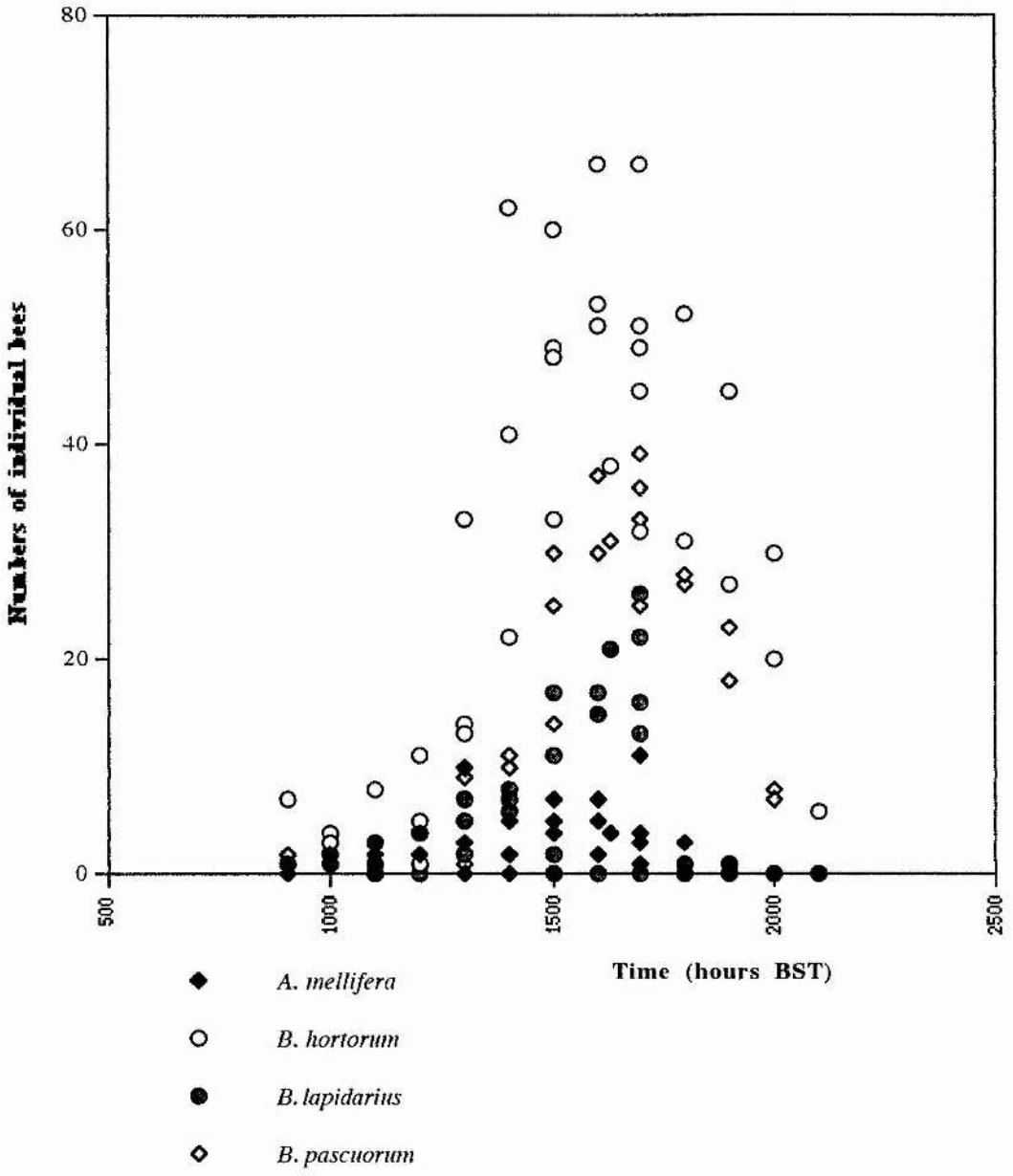


Fig. 3.3iii Changes in the mean numbers of the four most abundant bee species (*A. mellifera*; *B. hortorum*; *B. pascuorum*; and *B. lapidarius*.) foraging on field beans throughout the day (10/7-15/7/95).

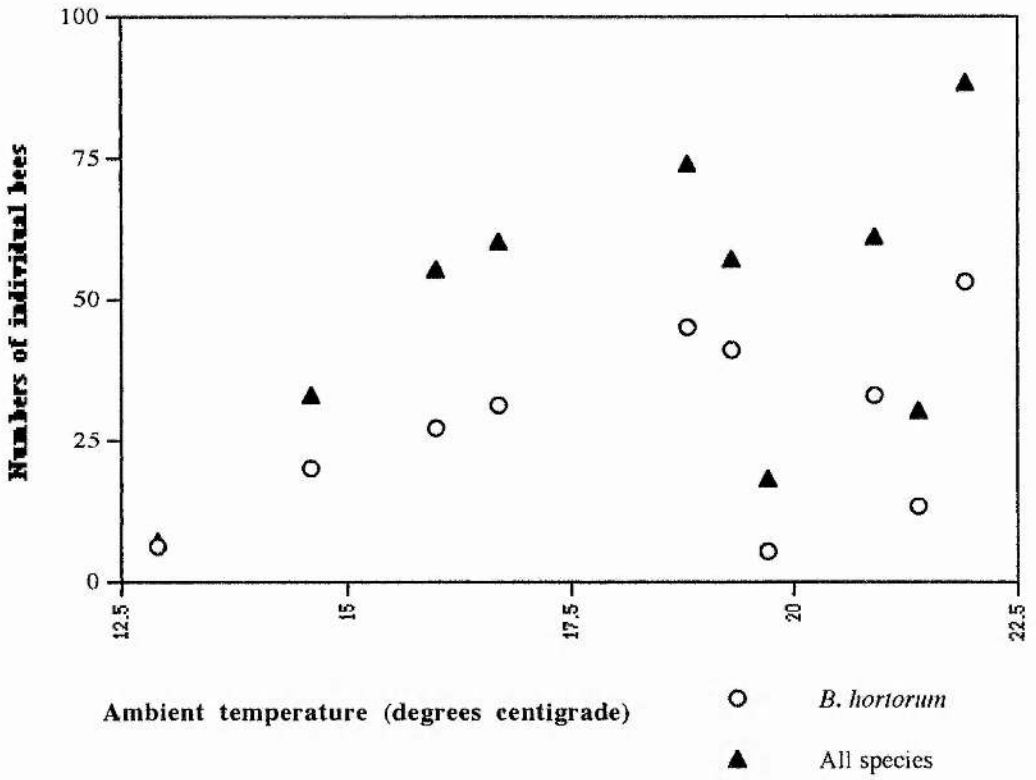
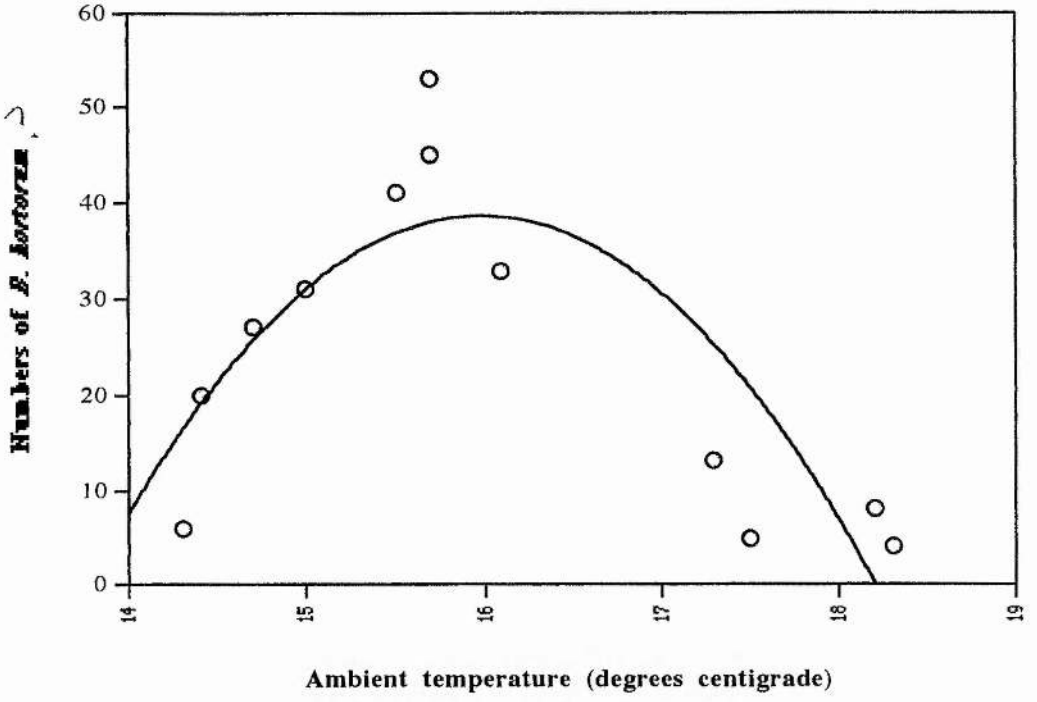


Fig. 3.3iv Numbers of individual bees of all species and of *B. hortorum* alone against ambient temperature (°C) 1/7-15/7/95.

The model most likely to fit this curve is a second-order polynomial, but when fitted to data over all days the effect is not statistically significant. A clear relationship is, however, apparent when separate regression analyses using the second-order polynomial function are performed for each day (for example, 11/7/95, Fig. 3.3v).



B. hortorum = $-7.881Ta^2 + 251.981Ta - 1975.472$

Fig. 3.3v Frequency of observations of *B. hortorum* with ambient temperature (°C) 11/7/95. For the above relationship, p = 0.002; R^2 = 73.7%.

Plots of numbers of individual bees (of all species and of *B. hortorum* alone) against mean nectar concentrations per sampling interval (n = 10+) from 1/7/95 to 15/7/95 show a strong trend towards increasing numbers of bees at higher nectar concentrations (Fig 3.3vi). This is not the case for a plot of bee numbers against nectar volumes (μl) over the same time period (Fig. 3.3vii). The extant data is not sufficient to show the decrease in bee activity that was observed on one or two very hot, dry afternoons when floral nectar was highly concentrated and difficult to extract from the bean flowers.

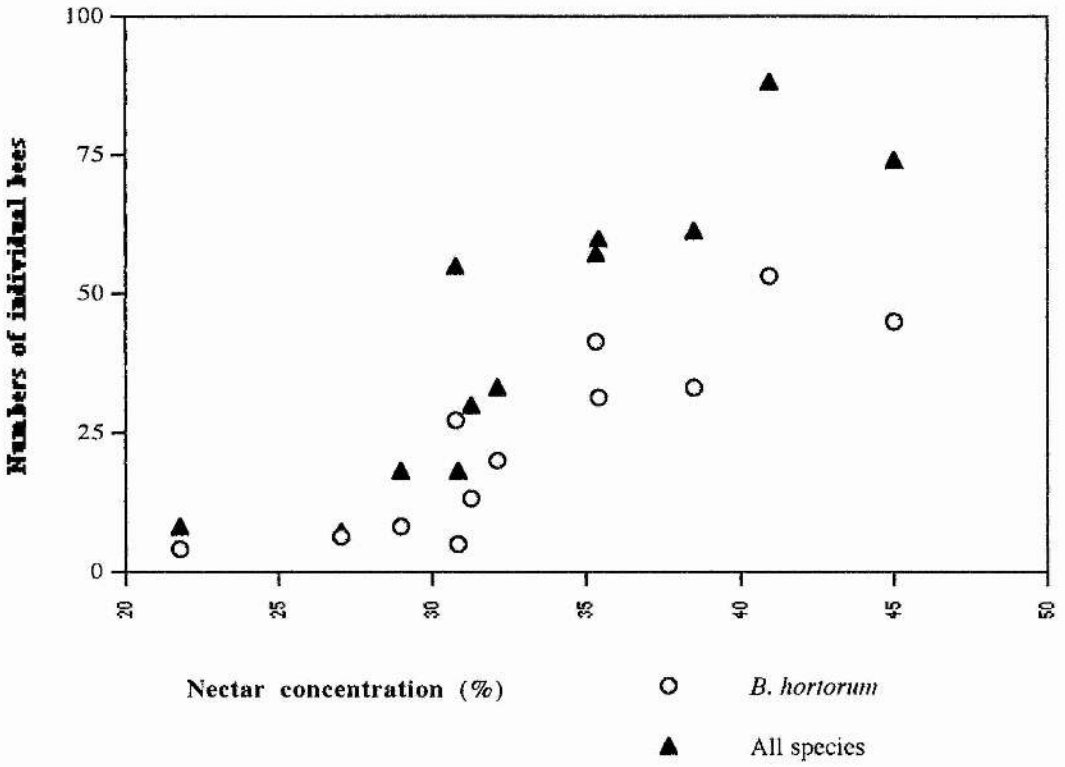


Fig. 3.3vi Numbers of individual bees of all species and of *B. hortorum* alone against nectar concentration (% dissolved sugars) 1/7-15/7/95.

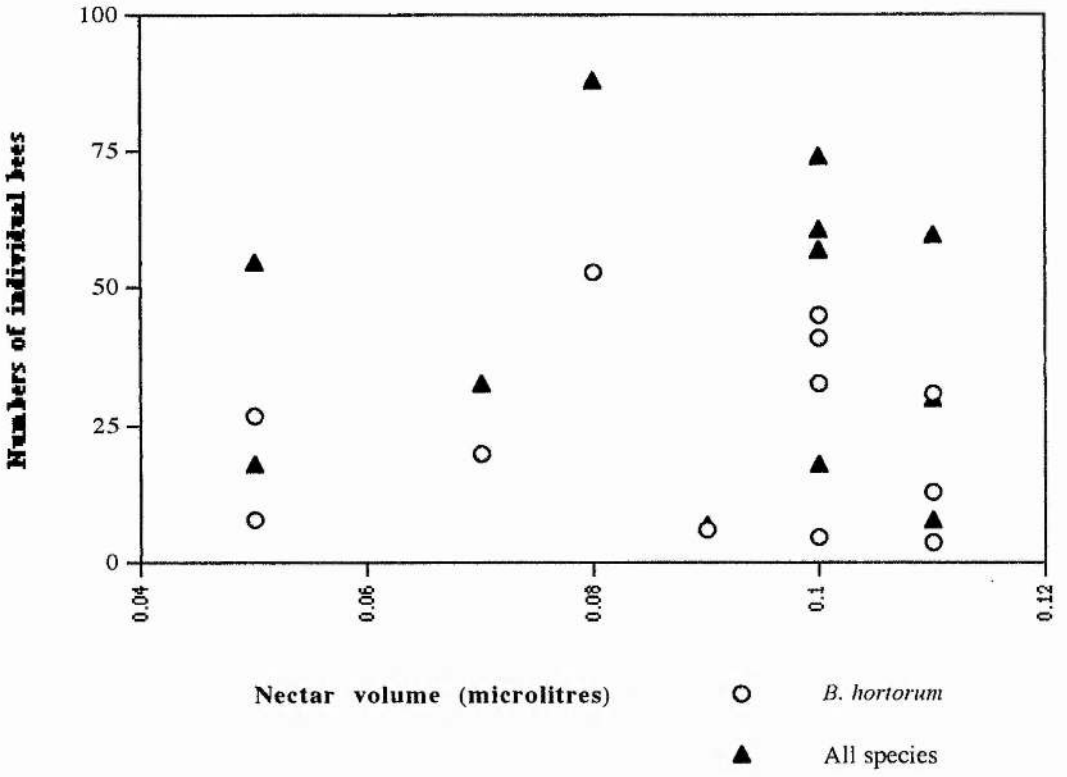


Fig. 3.3vii Numbers of individual bees of all species and of *B. hortorum* alone against nectar volume (μl) 1/7-15/7/95.

Plots of nectar concentration and volume against ambient temperature from the same dataset (i.e. means per sampling interval 1/7-15/7/95) suggest that temperature has no apparent effect on nectar volume. Nectar concentration, does show a positive relationship with ambient temperature (Fig. 3.3viii). The association between nectar concentration and nectar volume, which would be expected to be strongly positive, was not discernible from this dataset. Data regarding nectar characteristics are examined in greater detail above.

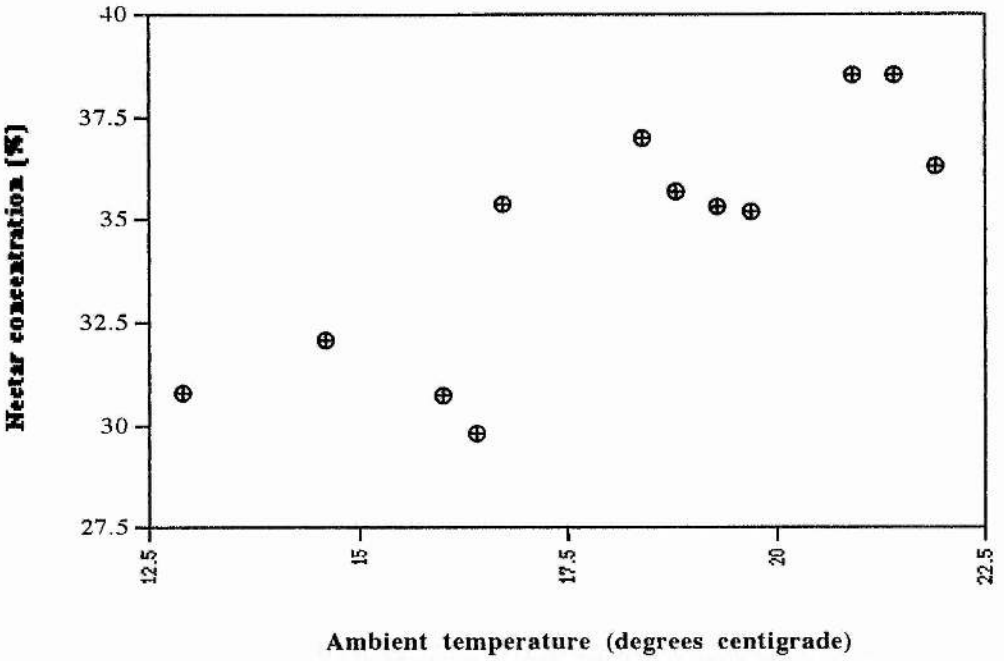
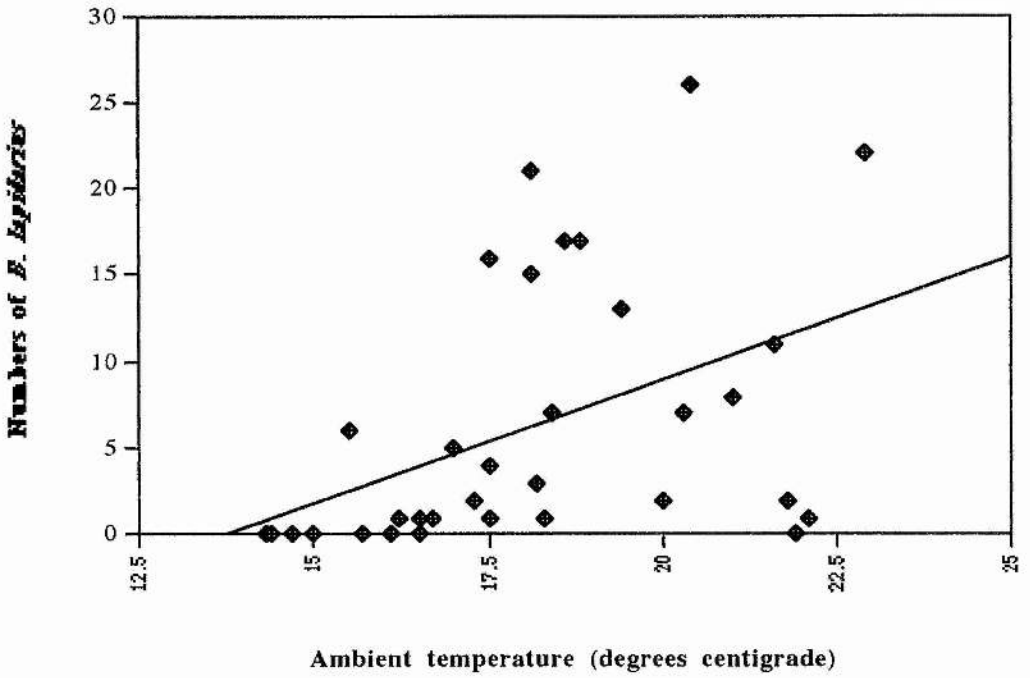


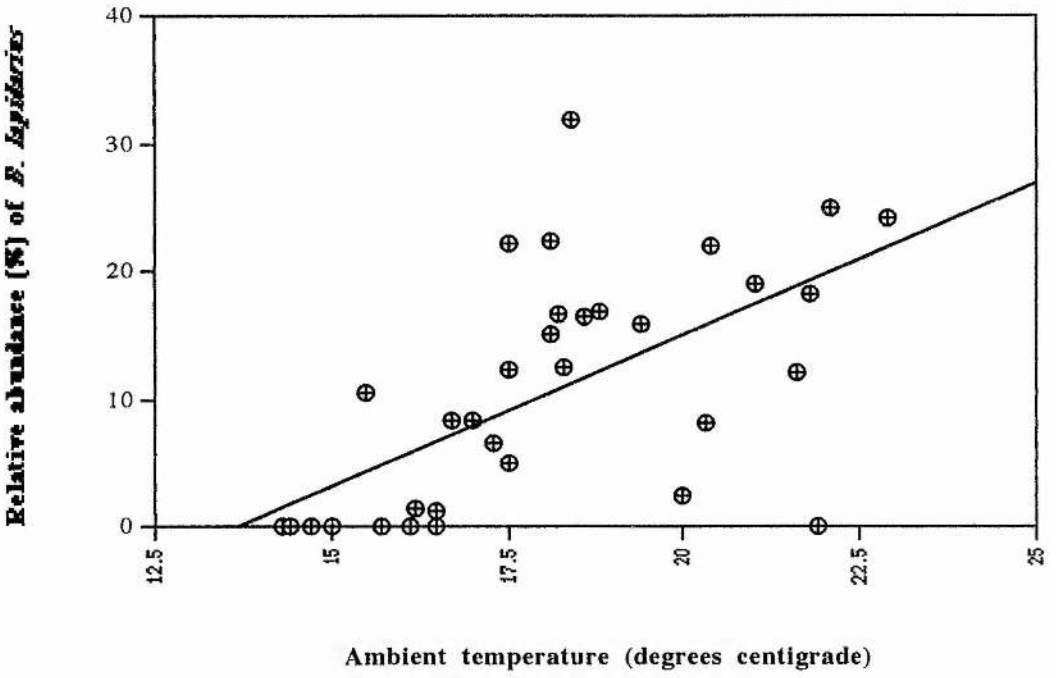
Fig 3.3viii Nectar concentration (% dissolved sugars) and ambient temperature (°C); means of all sampling intervals 1/7-15/7/95.

Despite the trend apparent in Fig 3.3iv, tests for association between environmental variables (temperature and humidity) and bee numbers on field beans were non-significant. However, where data for individual species and/or separate days were examined as isolated datasets, some statistically significant associations were discovered (e.g. Fig 3.3v). In addition, honeybee activity showed a positive response to increases in ambient temperature ($p = 0.05$, $R^2 = 28.5\%$), and a negative response to increases in ambient relative humidity ($p = 0.02$, $R^2 = 26.5\%$) across all days of observations. *B. lapidarius* activity showed a positive response ($p = 0.006$, $R^2 = 20.9\%$) to increased ambient temperature (see Fig 3.3ix). The percentage abundance of *B. lapidarius* also showed a significant effect ($p = 0.000$, $R^2 = 38.1\%$) of ambient temperature (Fig 3.3x).



Numbers of *B. lapidarius* = 1.429 (Ta) - 19.674

Fig. 3.3ix Numbers of *B. lapidarius* foraging on field beans and ambient temperature (°C) 10/7-15/7/95.



Relative abundance (%) of *B. lapidarius* = 2.373 (Ta) - 32.486

Fig. 3.3x Relative abundance of *B. lapidarius* on field beans (% of foraging community) and ambient temperature (°C) 10/7-15/7/95.

3.3ii Relative abundance of bees foraging on different cultivars

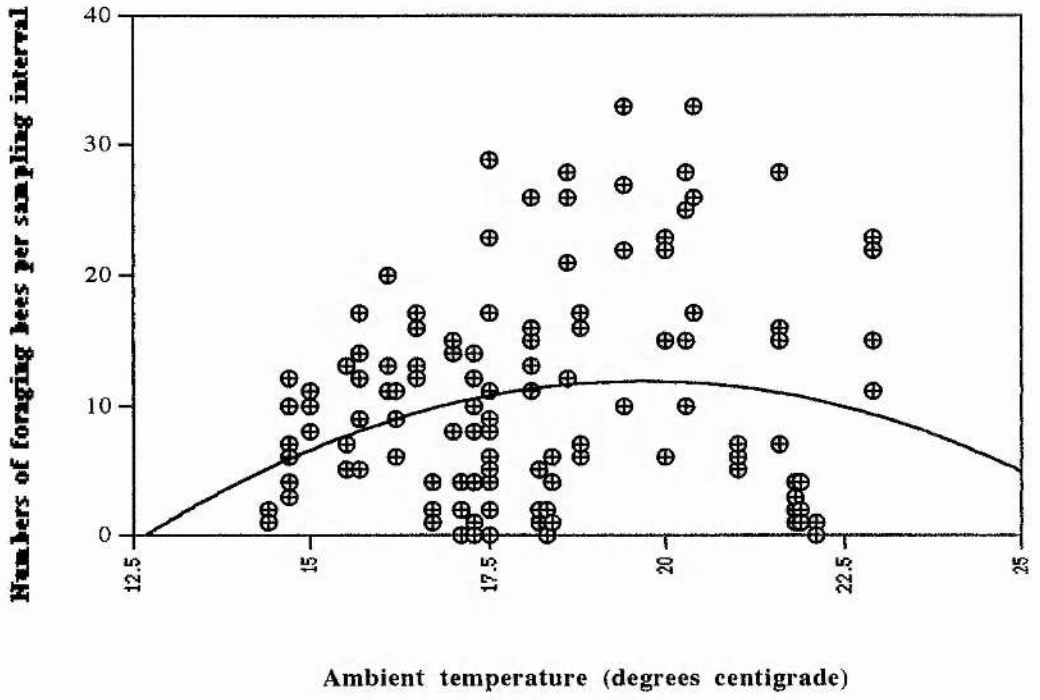
The tall late-flowering cultivars (Bourdon, Glacier, Maris Bead and Punch) bloomed concurrently between 10/7 & 15/7/95. Species counts were made at hourly intervals during this period. The resulting dataset provides the most complete picture of species structure obtained from field observations. Mean abundance data (for individual species and for total bee numbers on the four late-flowering cultivars) are given in Table 3.3. These data suggest that the Glacier and Maris Bead cultivars, which have a higher density of floral display at peak flowering (see Table 2.1) attract bumblebees in greater numbers than do Bourdon and Punch.

	Cultivar			
	Bourdon	**Glacier**	**Maris Bead**	**Punch**
Mean number of foraging bees observed at hourly intervals:				
All species:	9.40 +/- 1.48	11.09 +/- 1.58	11.29 +/- 1.37	8.06 +/- 0.90
Mean relative abundance (%) of different species at hourly intervals:				
A. mellifera	6.38 +/- 2.18	4.68 +/- 2.88	8.77 +/- 3.22	6.15 +/- 2.51
B. hortorum	51.65 +/- 5.16	60.03 +/- 4.99	57.98 +/- 3.52	54.33 +/- 4.81
B. lapidarius	10.48 +/- 3.52	12.90 +/- 3.39	5.80 +/- 1.98	10.3 +/- 2.54
B. lucorum	2.31 +/- 1.64	5.05 +/- 2.18	1.41 +/- 0.99	7.72 +/- 4.30
B. pascuorum	29.19 +/- 3.79	17.34 +/- 3.63	25.08 +/- 3.14	19.41 +/- 3.46

Table 3.3 Mean total bee numbers and mean relative abundance (% of foraging community) of the five most common bee species per sampling interval (observations during 20 minutes every hour) on field beans between 10/7 and 15/7/95.

One-way analysis of variance of these data could not find a significant difference between the total numbers of bees foraging on each of the four cultivars. The apparently higher total bee numbers on the two cultivars with higher floral density at peak flowering (Glacier and Maris Bead) were not statistically significant by analysis of variance ($p = 0.071$, $F = 3.32$).

The number of bees of all species foraging on these four cultivars between 10/7 and 15/7/95 were found to be significantly greater at higher ambient temperatures ($p = 0.049$, $R^2 = 2.8\%$). The relationship between total numbers of bees and ambient temperature implied by these data is illustrated in Fig 3.3xi.



Number of foraging bees = $-0.244\ (Ta)^2 + 9.579\ (Ta) - 82.318$

Fig 3.3xi Mean number of bees (all species) foraging on field beans observed during hourly 20 minute sampling intervals 10/7-15/7/95.

There were significant differences between the total numbers of bees observed on different days between 10/7 and 15/7/95 ($p = 0.003$, $F = 4.2$). Mean ambient temperatures varied across days ($p = 0.000$, $F = 28.7$), for example the mean ambient temperature on 11/7 was 16.3 °C, while that for 15/7 was 19.6 °C. The four environmental variables measured during this period, i.e. ambient temperature and relative humidity, and temperature and humidity prevailing at the surface of the flower, were strongly associated, as would be expected. For example, ambient temperature was strongly predictive of flower surface temperature (positive relationship; $p = 0.000$, $F = 868.3$), of ambient relative humidity (negative relationship; $p = 0.000$, $F = 205.2$), and of relative humidity at the surface of the flower (negative relationship; $p = 0.000$, $F = 211.98$).

Separate analyses of bee numbers were carried out for the five most common bee species observed foraging on the four late-flowering cultivars. Numbers of flower visits by honeybees were found to be strongly and positively associated with ambient temperature ($p = 0.000$, $R^2 = 10.6\%$), but were not influenced by cultivar. Likewise, the numbers of *B. hortorum* and *B. lapidarius* foraging on the crop were influenced by environmental variables but not by cultivar. *B. hortorum* activity showed no discernible temperature affect, but was lower at higher relative humidities ($p = 0.03$, $R^2 = 3.5\%$). *B. lapidarius* was more abundant at higher ambient temperatures ($p = 0.000$, $R^2 = 12.0\%$). *B. lucorum* showed no preference for any of the four cultivars, but was more active at higher humidity levels ($p = 0.015$, $R^2 = 4.2\%$), corresponding to the fact that most *B. lucorum* individuals were observed during the evening (18:00 - 20:00 hours BST). Numbers of *B. pascuorum* did not appear to be directly affected by the environmental variables, and did not vary significantly between cultivars, but they did show a significant increase throughout the day until approximately 17:00-18:00 hours BST (Fig 3.3xii). No predictor of visits by *B. pratorum* or *B. terrestris* could be found among the known variables. These species were relatively rare on the plot and data concerning them are sparse.

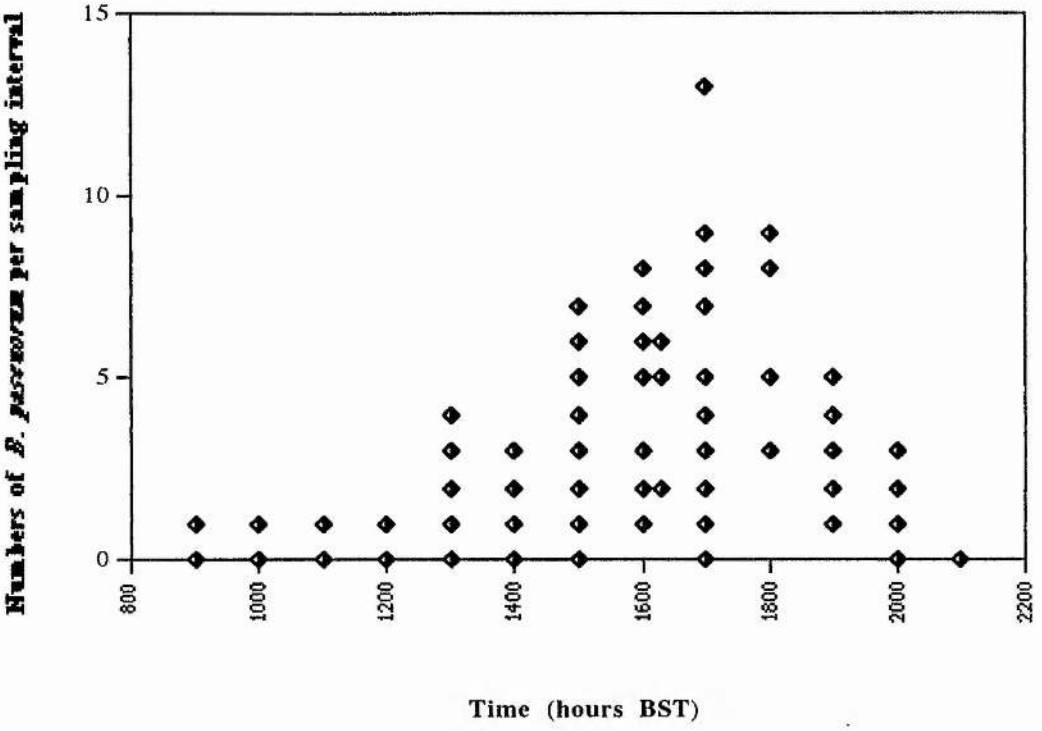


Fig 3.3xii Numbers of *B. pascuorum* foragers on late-flowering field bean cultivars throughout the day between 10/7 and 15/7/95. Datapoints refer to actual counts obtained during hourly timed walks of 20 minutes duration.

Analysis of relative abundance rather than absolute numbers of different species foraging on the crop gave a slightly different picture. The relative abundance of *A. mellifera* foragers was greater at higher ambient temperatures ($p = 0.021$, $R^2 = 4.0\%$) and decreased through the day ($p = 0.000$, $R^2 = 12.1\%$); see Fig 3.3xiii. The proportion of honeybees in the foraging community was greatest in the morning and reached a peak of up to 50% between 09:00 and 13:00 hours BST, before long-tongued bumblebees became more active on the plot. Absolute numbers of honeybees were, however, highest during the middle of the day (see Fig 3.3iii). This may be connected to the fact that honeybees collected nectar primarily from extrafloral nectaries, which offer a nectar reward during the morning before the field bean flowers are open. It may also relate to the possibility that the activity of

honeybees on field beans is more strongly dependent on diurnal temperature changes than other species in the foraging community.

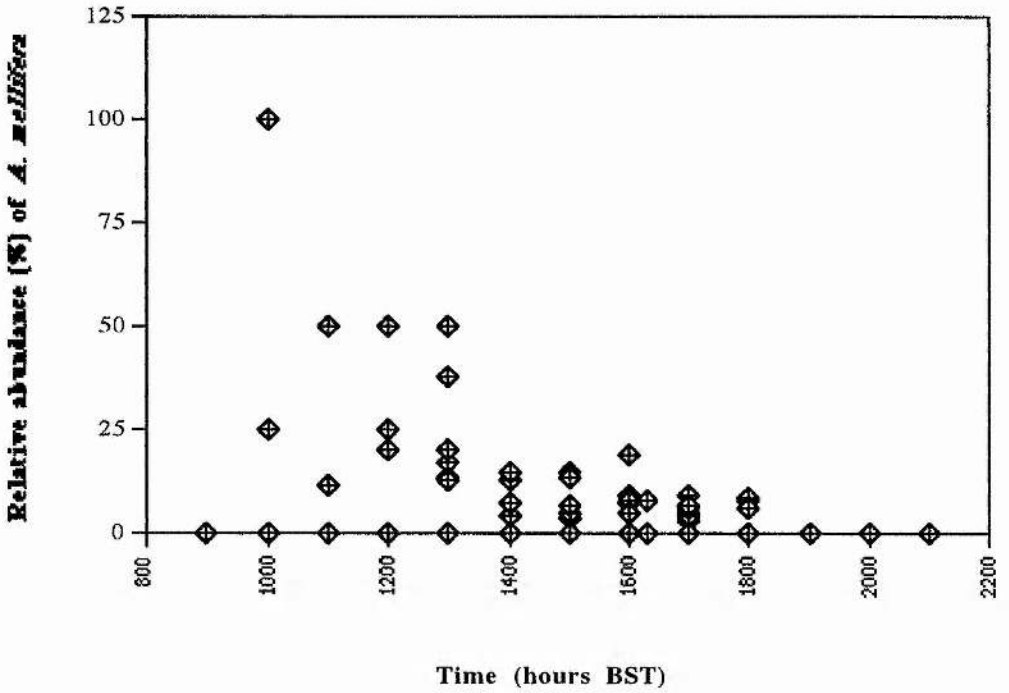
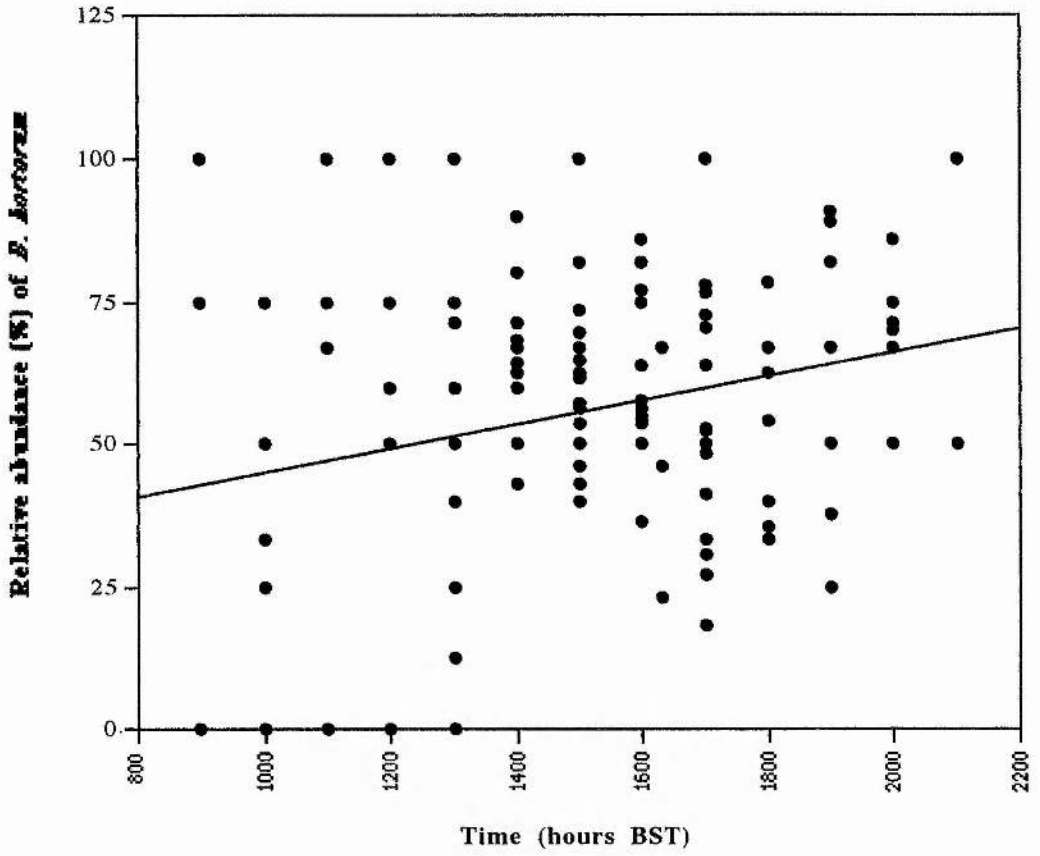


Fig 3.3xiii Changes in the relative abundance (% of total number of bees) of *A. mellifera* foragers on field beans throughout the day 10/7-15/7/95.

In contrast, the relative abundance of *B. hortorum* tended to increase throughout the day (Fig 3.3xiv). There was a significant positive effect of temperature on the relative abundance of *B. hortorum* ($p = 0.019$, $R^2 = 4.2\%$) and *B. lapidarius* ($p = 0.004$, $R^2 = 8.4\%$). The relative abundance of *B. lucorum* was higher at lower ambient temperatures ($p = 0.038$, $R^2 = 4.3\%$) reflecting the observation that this species tended to be more active in the evenings. appeared to change significantly only with the time of day ($p < 0.000$), indicating that it is responding to some other variable associated with the diurnal cycle.



Percentage abundance of *B. hortorum* = 0.021 (Ta) + 23.450

Fig 3.3xiv Changes in the relative abundance (%) of *B. hortorum* in the foraging community throughout the day 10/7-15/7/95.

According to the data collected in the present study, there is no difference in levels of bee activity on the four late-flowering cultivars Bourdon, Glacier, Maris Bead and Punch. No difference could be detected in the relative abundance of bees foraging on all cultivars between 10/7 and 15/7 that could not be accounted for by differences in flowering stage. Analysis of variance of the mean percentage distribution of different species on different cultivars did not show an effect of cultivar on foraging preferences by different species of bee between 10/7 and 15/7/95.

3.3iii Variations in species composition of the field bean foraging community

During the first part of the flowering season, *B. pascuorum* was the most frequent visitor to field bean flowers. On 26/6 and 27/6/95, when Scirocco was at peak flowering, *B. pascuorum* constituted 44 - 47 % of all bees (including honeybees and bumblebees) observed on the plot; *B. hortorum* represented only 34 - 37 % of all observations during this time. *B. lapidarius* was at first an infrequent visitor to the plot, and during the first three days of observation only two *B. lapidarius* individuals were recorded. Both were small workers and basked on the bean leaves but were not seen to forage. *B. pratorum* was not observed on the field beans until 11/7/95.

From 1/7/95 *B. hortorum* was the dominant nectar forager and *B. pascuorum* took second place. Figure 3.3xv illustrates this shift using data extracted from a dataset concerning foraging rates, which, unlike the timed walk data, were collected at intervals throughout the flowering season. It can be seen that the frequency of *B. lapidarius* visits increased markedly towards the end of the flowering period (12/7-15/7/9). More detailed species counts would need to be made in order to ascertain whether the shift suggested by field observations and by the data in Fig 3.3xv was statistically significant or simply random variation. Shifts of relative abundance in insect communities may be a seasonal phenomenon; alternatively, they may be triggered by changes in environmental factors. Extant data do not allow further reliable analysis of species composition.

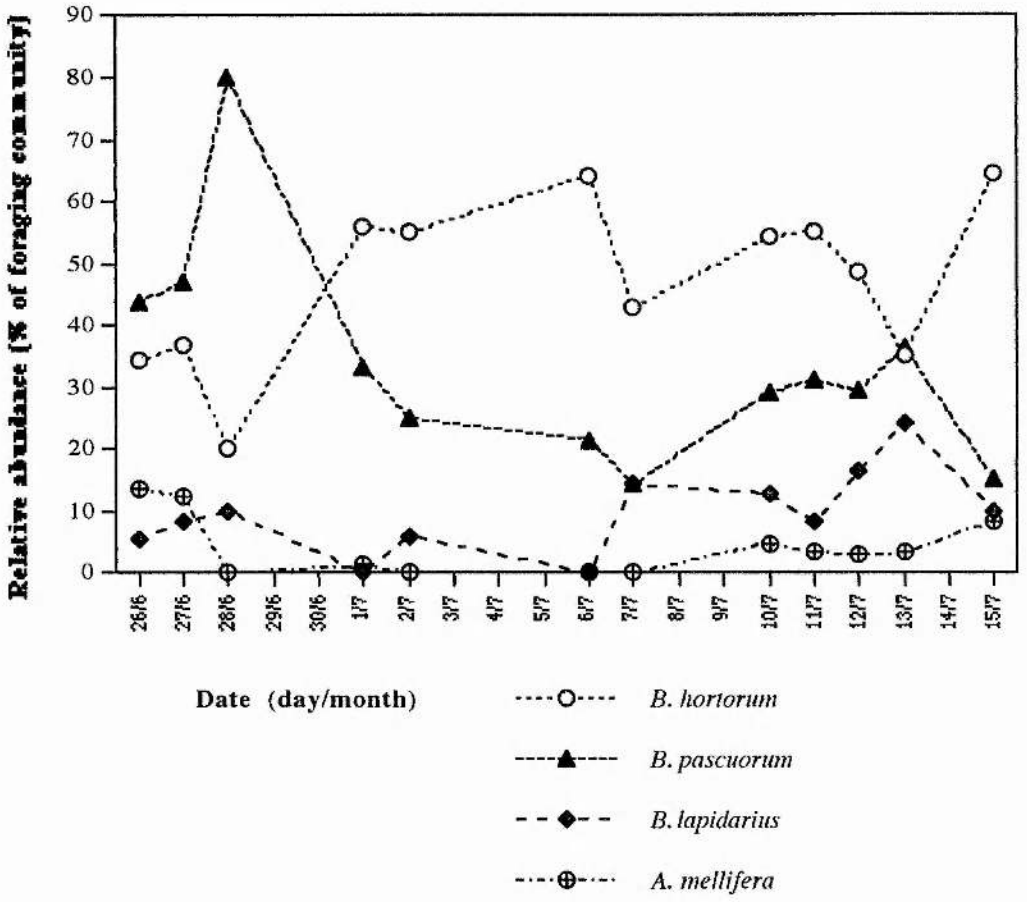


Fig 3.3xv Relative abundance (percentage of foraging community) of four bee species foraging on field beans 26/6-15/7/95, taken from the foraging rate dataset. N > 20 for all samples.

Chapter 4

Results: *Phacelia*

4.1 Nectar profiles for *P. tanacetifolia*
4.2 The behaviour of bees on flowers, and rates of flower visitation
4.3 The size and species composition of the bee community on *Phacelia*

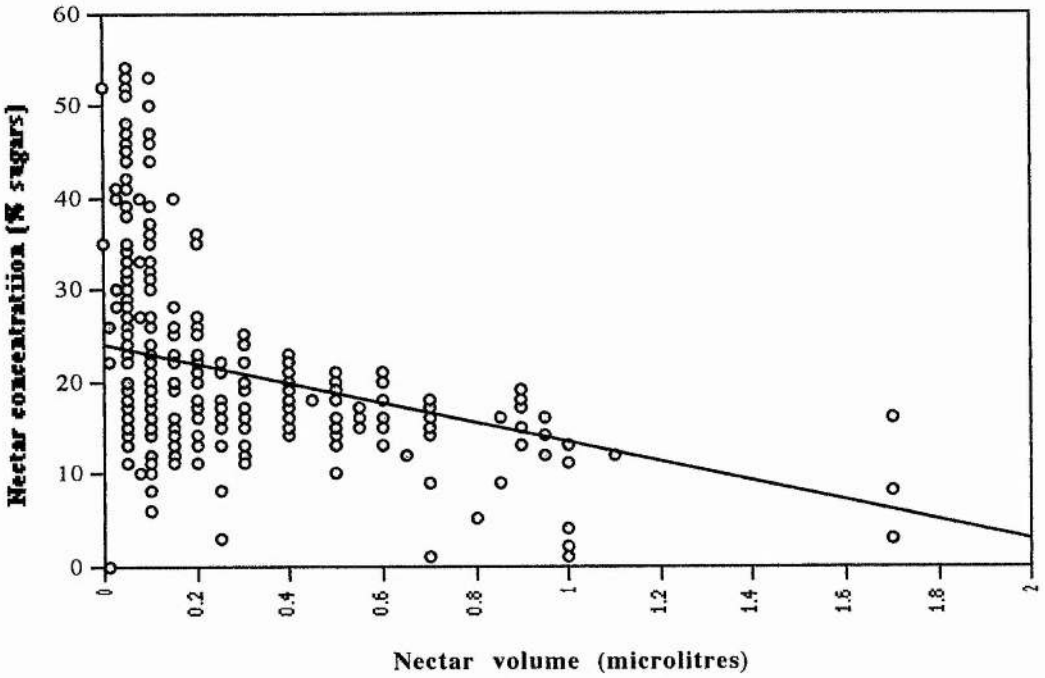
4.1 Nectar profiles for *P. tanacetifolia*

4.1i Nectar concentration and volume

Like field beans, *Phacelia* flowers produce small volumes of relatively dilute nectar. The average nectar sample from a single *Phacelia* floret was 0.12 μl at a concentration of 18.6% dissolved sugar solids. There was great spatial and temporal variation in the volume and concentration of *Phacelia* nectar in the study crop. *Phacelia* nectar shows a strong pattern of change in both these characteristics throughout the day, and provides a contrast to the field bean nectar profiles discussed in Chapter 3.

Comprehensive nectar profiles were obtained for *Phacelia* from 26/7 to 28/7/95. As expected, there was a strong negative relationship between mean nectar concentration and mean nectar volume ($p = 0.000$, $R^2 = 15.7\%$; $r = -0.8$). Fig. 4.1i shows that small volumes of nectar show greater variation in nectar volume than larger volumes, and that from the majority of nectar-containing florets (i.e. "positive" samples) tested throughout the day, small volumes were recorded.

Of the four environmental variables recorded throughout the *Phacelia* study - mean ambient temperature (°C; T_a) and relative humidity (%; RH_a), and mean flower surface temperature (T_f) and relative humidity (RH_f) - all were found to be good predictors of nectar volume and concentration.



Concentration = -10.656 (volume) + 24.077

Fig. 4.1i The relationship between nectar concentration (% dissolved sugars) and nectar volume (μl) in *Phacelia* 19/7-28/7/95 (N = 859).

Table 4.1i shows the values of R^2 for all linear combinations of nectar characteristics with environmental variables over all days of study and for 28/7 only (for all relationships, p = 0.000). As expected, there was a strong positive relationship between ambient temperature and relative humidity (p = 0.000, R^2 = 73.9%). Figs 4.1ii and 4.1iii illustrate the effect of temperature on nectar volume and concentration on 28/7. The highest nectar volumes were found at lower ambient temperatures, while nectar concentration peaked at peak ambient temperature.

Variable	R^2 (%) [Vol. (μl)]		R^2 (%) [Conc. (%)]	
	28/7 only	19/7-28/7	28/7 only	19/7-28/7
T_a	16.3	6.3	55.4	16.1
T_f	15.6	6.7	51.6	16.8
RH_a	13.1	8.7	48.4	23.8
RH_f	13.2	8.3	50.0	21.9

Table 4.1i Results of linear regressions of environmental variables on *Phacelia* nectar characteristics: 28/7 (N = 330) and 19/7-28/7/95 (N = 859).

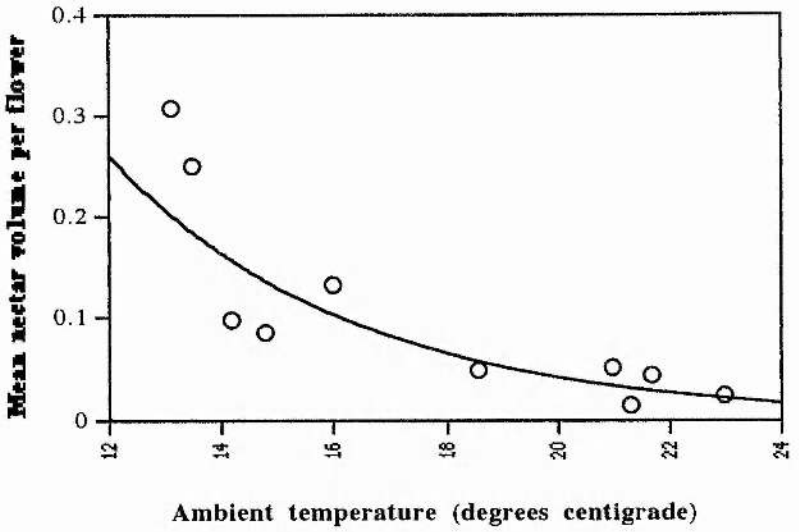


Fig. 4.1ii Mean nectar volume (μl) per *Phacelia* floret and mean ambient temperature (°C) on 28/7/95 (N = 330). The data appear best described by an exponential line.

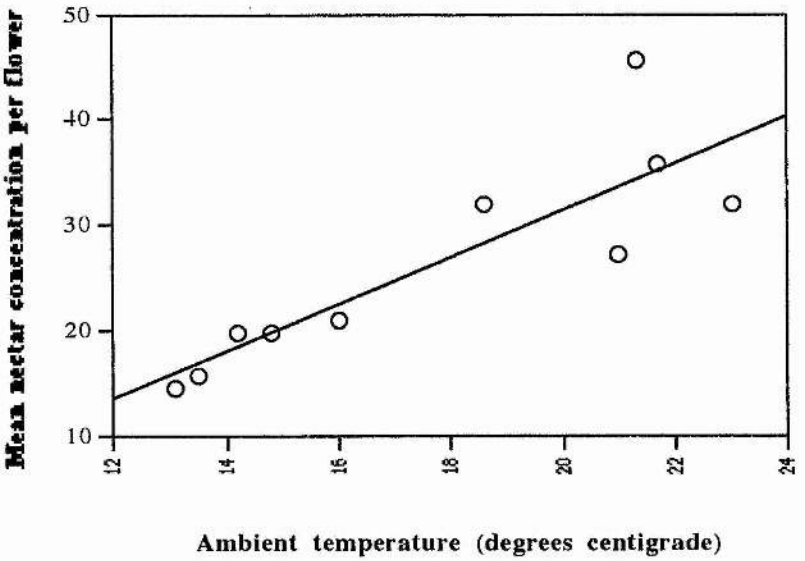


Fig. 4.1iii Mean nectar concentration (% sugars) per *Phacelia* floret and mean ambient temperature (°C) on 28/7/95 (N = 330). The data appear best fitted by a straight line.

4.1ii The spatial and temporal distribution of nectar

Typical diurnal changes in mean nectar volume and concentration are illustrated in Figs 4.1iv and 4.1v. The largest nectar volumes were found in the early morning (06:00-08:00 hours BST) and early evening (18:00-21:00 hours). Nectar concentration appeared to reach a peak in the middle of the afternoon (around 16:00 hours).

The proportion of negative samples obtained in any sample (i.e. the number of florets containing no nectar in a sample of consistent size) varied with the time of day (Fig. 4.1vi). In the early morning negative samples were infrequent (less than 15 per cent) while during the middle hours of the day (10:00-16:00 hours) the majority of florets gave negative samples.

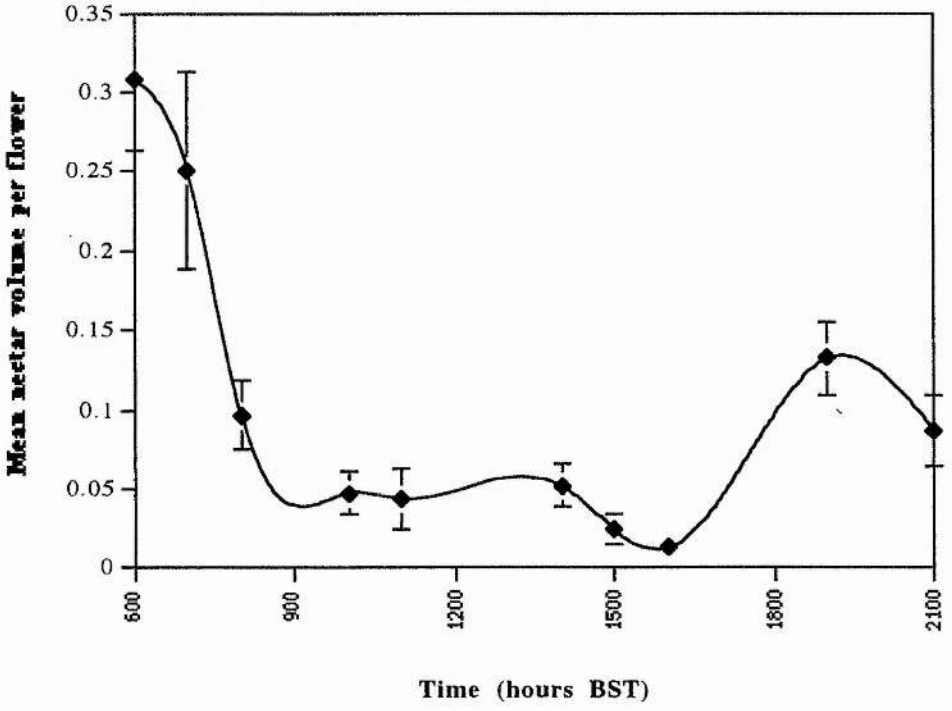


Fig. 4.1iv Diurnal changes in the mean nectar volume (μl) per *Phacelia* floret on a typical day of sampling, 26/7/95 (N = 259).

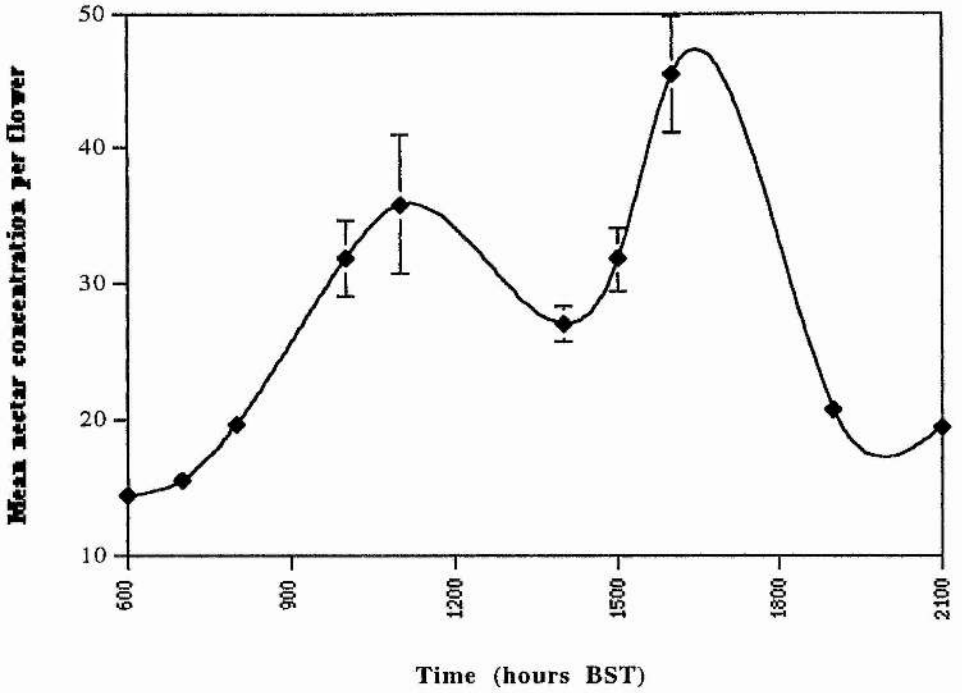


Fig. 4.1v Diurnal changes in the mean nectar concentration (% sugars) per floret in *Phacelia*, 26/7/95 (N = 259).

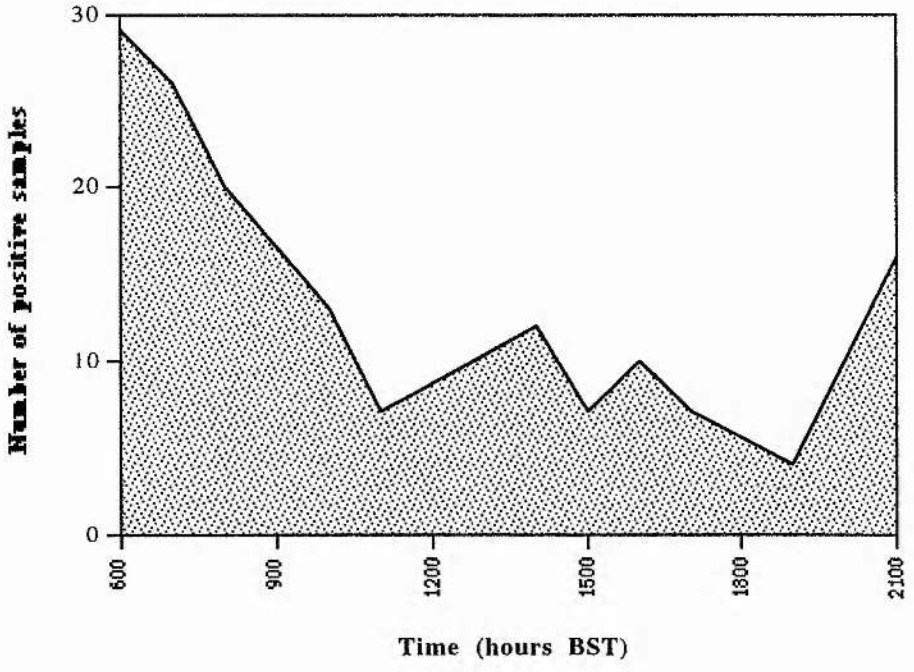


Fig 4.1vi The distribution of positive (shaded) and negative (unshaded) nectar samples in *Phacelia*, 26/7/95 (N at each sampling interval = 32).

A bee may be able to extract trace nectar volumes from a *Phacelia* floret which yields none to the microcapillary, and it would be interesting to analyse nectar on a finer scale so as to determine at which point a nectar reward too small to be collected by a microcapillary may be "rewarding" to a bee. If a significant proportion of these florets are unrewarding in fact as well as in appearance to the observer, this might throw light upon the questions of the remote nectar perception abilities of bumblebees, and of the effects of recent rewards upon future foraging decisions and inter flower movements. At all events, the period during which the frequency of apparently "empty" florets was highest coincided with the period of greatest activity by bees ($p = 0.011$, $R^2 = 49.0\%$; see Fig. 4.1vii).

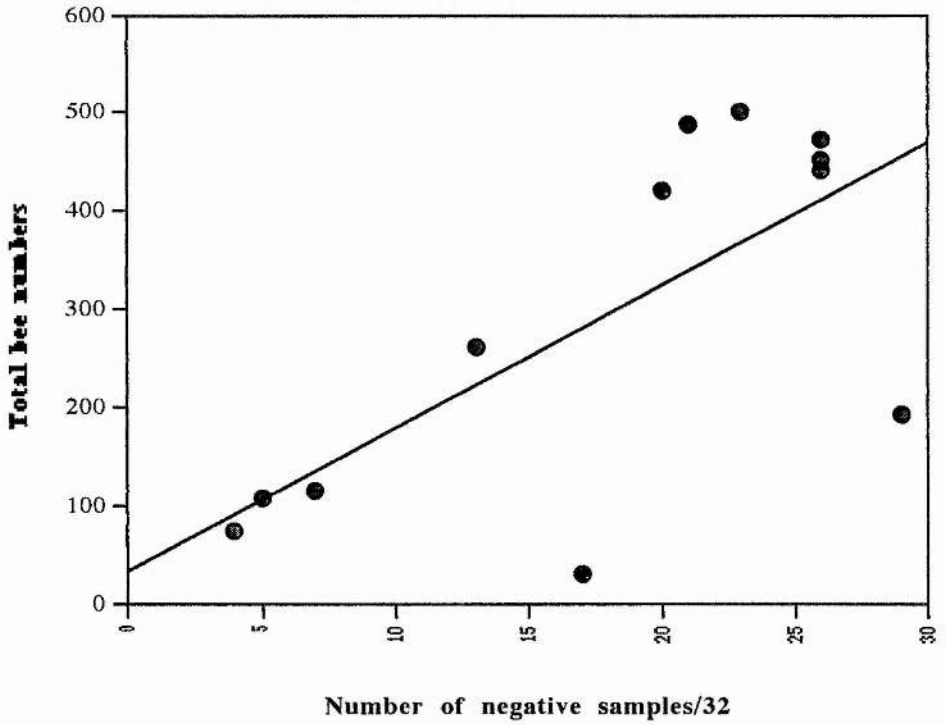


Fig. 4.1vii The relationship between the number of foraging bees on *Phacelia* at hourly intervals and the frequency of negative nectar records in a sample of 32 florets, 26/7/95.

4.1iii Sheltered and emergent flower heads

In a sample of 100 florets, 50 of which were taken from emergent flower heads (i.e. protruding above the crop and receiving full sun) and 50 from sheltered flower heads (i.e. shaded by emergent plants of greater height), there was found to be a significant

difference in nectar concentration ($p = 0.001$, $F = 11.82$) between sheltered and emergent flowers. Florets on sheltered flower heads had more dilute nectar (mean nectar concentration = 15.9% sugar solids) than those on emergent flower heads (mean concentration = 20.3%). There was, however, no significant difference between the mean nectar volumes of each group. If this result reflects a real difference in the quality of nectar in sheltered and emergent flowers, it may relate to the peculiar observation that small *B. pascuorum* workers appeared on occasion to restrict flower visits to the smaller, shaded flower heads during the middle of the day.

4.1iv Newly-opened, mature and senescing florets

In newly-opened florets (identified by the curled, protected position and the intact pollen load of the anthers) and in senescing florets (in which the corolla had begun to shrink and to collapse inwards) nectar was less concentrated than in mature (or fully open) florets. Mature florets had an average nectar concentration of 19.6% ± 0.8, while the nectar in newly-opened and senescing florets had a mean concentration of 16.6% ± 0.9. This difference was significant ($p = 0.029$, $F = 4.94$) and may be explained by the more protected microclimate provided by the slightly incurved corollas of newly-opened or senescing florets. There was no significant difference in nectar volumes among these groups.

4.2 The behaviour of bees on flowers, and rates of flower visitation

4.2i Flower visitation behaviour

The data presented here refer only to visits to the front of the floret to collect nectar and/or pollen. Nectar robbing was not once observed on *Phacelia*, and the corollas are sufficiently shallow as to make it of little value as a foraging strategy for short-tongued bees (such as *B. terrestris* and *B. lucorum*) on this crop. Most bumblebee species appeared to gather pollen incidentally while probing for nectar apart from *B. pascuorum* which was often observed "scrabbling" over the anthers for pollen. *A. mellifera* would alight on the anthers and "rake" the pollen. *B. lucorum*, *B. hortorum* and *B. pascuorum* often carried full loads of *Phacelia* pollen, which was a distinctive blue in colour. At intervals, bees scraped pollen trapped in their body hairs into their corbiculae. Very small bumblebee workers of *B. pascuorum* were frequently observed to concentrate their foraging on the small, low-growing inflorescences

beneath the main canopy. Relatively few bees visited the lower flowers, and this was especially true of *B. lucorum* and *B. lapidarius*.

4.2ii Inter flower movements

Patterns of inter flower movement within the *Phacelia* crop between 19/7 and 28/7/95 were highly variable. Some bees flew relatively long distances between successive inflorescences while others flew to the next nearest one; for example, 5 of 19 bumblebees observed between 11:00 and 14:00 hours on 20/7 flew a distance of three metres or more between flower heads, while the rest tended to fly between adjacent inflorescences in the field. Bumblebees often approached a flower head, even landing briefly, only to reject it at the last moment. The number of rejected inflorescences was often very high, e.g. one *B. hortorum* was observed to reject 7 heads in a row (24/7).

4.2iii Rates of flower visitation

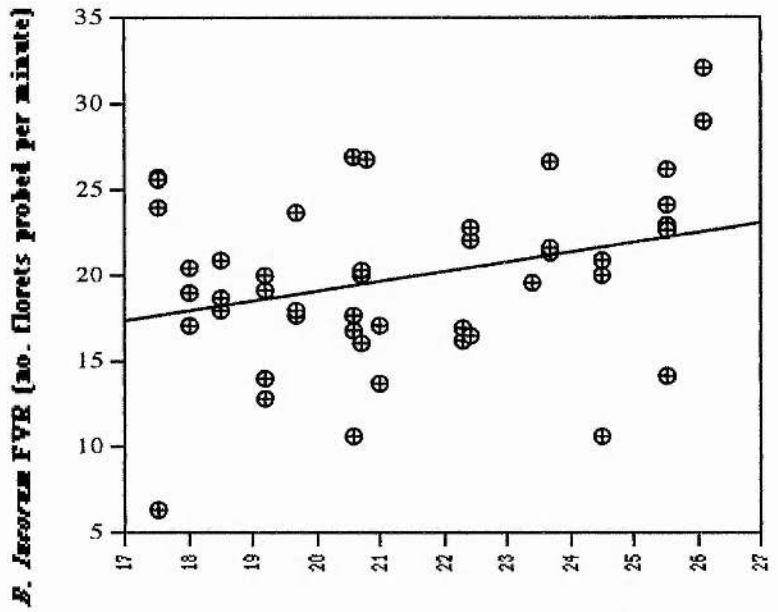
Estimates of flower visitation rates (FVR, or mean number of florets probed per minute) on *Phacelia* were obtained for *B. lapidarius*, *B. lucorum*, *A. mellifera*, *B. pascuorum*, *B. hortorum*, and *B. pratorum*. Bee species had a highly significant effect on FVR ($p = 0.000$, $F = 4.74$, $N = 135$), which was more marked still between honeybees and bumblebees ($p = 0.000$, $F = 17.19$). *B. lucorum* and *B. lapidarius* have the highest rates of flower visitation, probing on average 19-20 florets (on a variable number of inflorescences) per minute. *B. hortorum* and *B. pascuorum* were significantly slower, probing on average only 16-17 florets per minute, while *A. mellifera* visited, on average, only 8 florets per minute. Because of the small sample size for *B. terrestris*, the estimate for this species' FVR on *Phacelia* must be considered unrepresentative. A larger honeybee sample would also have been preferable. Bumblebee queens appeared to have much higher rates of probing and flower visitation. One *B. lucorum* queen averaged 27.3 florets per minute over a two minute observation period on 27/7.

Species	N	Mean time per floret (sec's)	FVR (florets per minute)
A. mellifera	6	8.28 +/- 1.18	7.82 +/- 0.83
B. hortorum	21	4.24 +/- 0.35	15.86 +/- 1.26
B. lapidarius	38	3.48 +/- 0.19	19.26 +/- 1.13
B. lucorum	47	3.29 +/- 0.18	19.87 +/- 0.74
B. pascuorum	14	4.30 +/- 0.52	16.71 +/- 2.12
B. pratorum	5	4.33 +/- 0.66	15.06 +/- 2.01
B. terrestris	2	2.82 +/- 0.52	22.03 +/- 4.03
Bumblebees	127	3.65 +/- 0.13	18.52 +/- 0.56

Table 4.1 Mean flower visitation rates of different bee species, and of bumblebees as a group, on *Phacelia* between 19/7 and 28/7/95. FVR = mean number of florets probed per minute. N = sample size. These estimates include flight time between successive inflorescences.

Environmental variables (ambient temperature and relative humidity) could not be shown to influence FVR across species. Ambient temperature did however, have a significant effect on flower visitation in *B. lucorum*. This species probed slightly more florets per minute at higher ambient temperatures ($p = 0.035$, $R^2 = 9.5\%$, $N = 47$). This relationship is illustrated in Fig. 4.2i. There were no detectable direct effects of environmental variables or time of day on FVR for any other species.

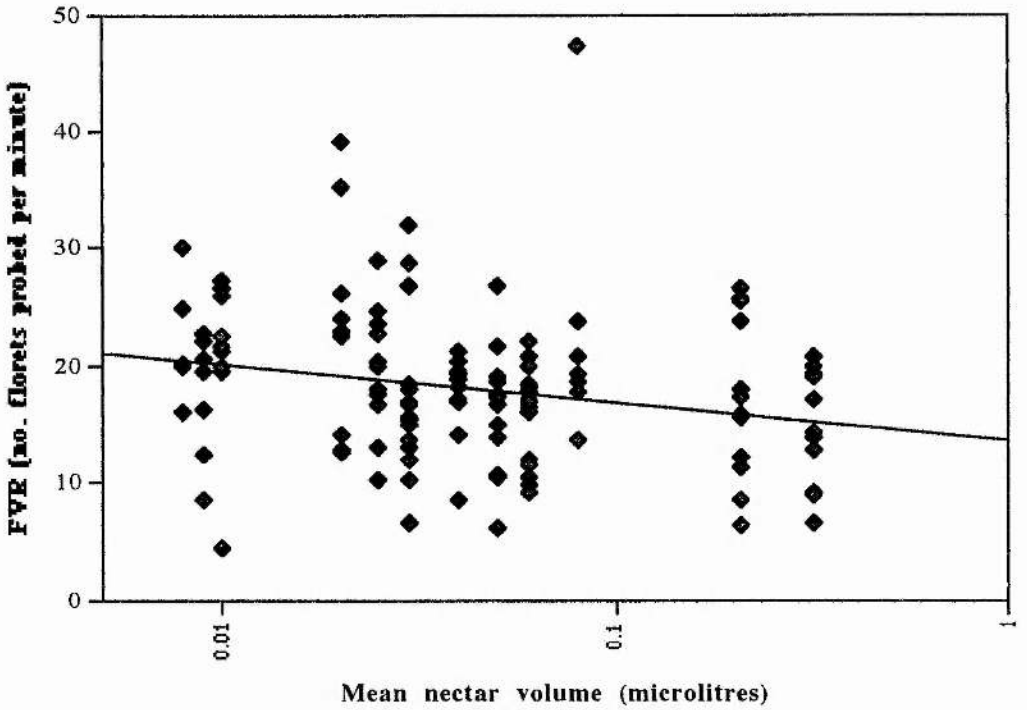
Multiple regression of FVR on *Phacelia* nectar characteristics (mean nectar volume and concentration per sampling interval where $N = 30$) showed a slight but significant effect of nectar volume ($p = 0.020$, $R^2 = 4.0\%$) on the mean number of florets probed per minute across all bee species (see Fig. 4.2ii).



No. florets / minute (*B. lucorum*) = 0.569 (Ta) + 7.673

Fig. 4.2i Influence of ambient temperature, T_a (°C), on the number of *Phacelia* florets probed per minute (FVR) by *B. lucorum*. N = 47.

Nectar concentration had no discernible effect. Both mean nectar volume and mean nectar concentration were highly correlated with ambient temperature (°C) across all days of the *Phacelia* study (19/7-28/7/95). For mean nectar volume and ambient temperature, p = 0.000, R^2 = 25.3%; for mean nectar concentration and temperature, p = 0.000, R^2 = 18.1%. There was also a strong negative association between the concentration and volume of *Phacelia* nectar (p = 0.000, R^2 = 54.1%). The increase in FVR for *B. lucorum* associated with higher ambient temperatures (Fig. 4.2i) may be due to the fact that lower nectar volumes at high T_a decrease the handling time for each individual floret.



No. florets / minute = -3.231LOG(nectar volume) + 13.655

Fig 4.2ii Influence of *Phacelia* nectar volume (sampling interval means) on FVR (number of florets probed per minute) across all bee species. N = 133.

4.2iv Numbers of florets probed per inflorescence

Bees never probed all florets on an inflorescence (mean number of mature, open florets per inflorescence = 28.5 distributed between an average of 5 fronds; N = 12). The incidence of probing on an inflorescence was highly variable for the majority of the 133 foragers observed. On one inflorescence a large number of florets might be probed (the maximum number probed on one flower head = 35 by *B. terrestris* on 28/7), while just one floret might be sampled on the next. Field observations suggested that probing just one floret per inflorescence was associated with greater distances travelled between successive flower heads, particularly for *B. pascuorum*

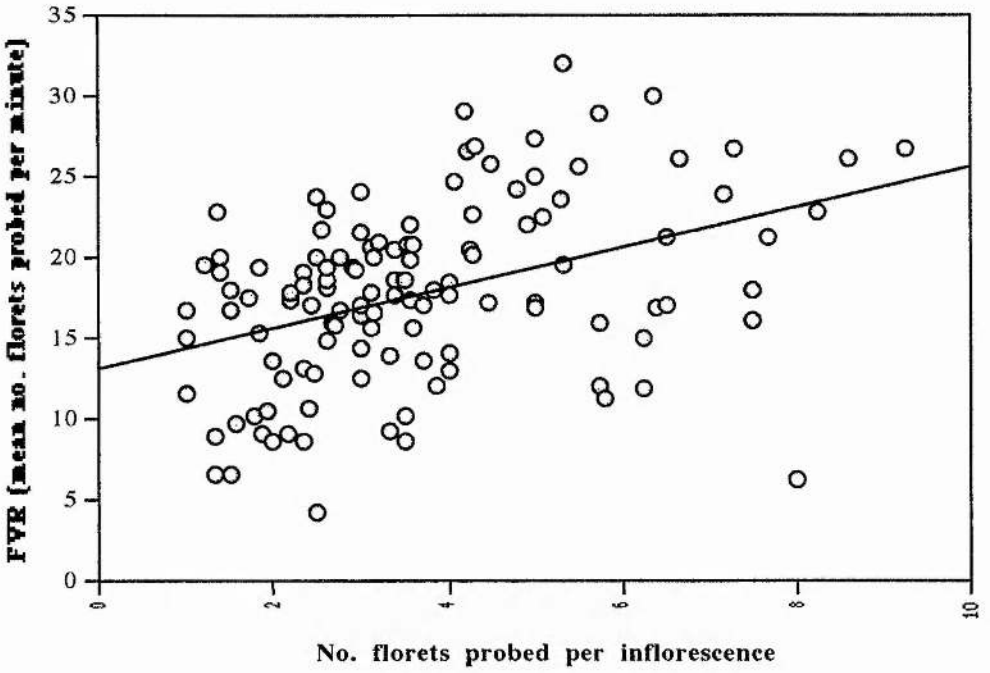
and *B. hortorum* on 19/7. This eventuality would be compatible with the arguments of Pyke (1978) which propose that low rewards within a patch prompt a forager to travel a greater distance in search of the next reward, but unfortunately insufficient data were collected to allow this possibility to be investigated. Analysis of variance of the number of individual florets probed per inflorescence found a significant effect of bee species ($p = 0.020$, $F = 2.63$). The results of this test are given in Table 4.2 below. *B. hortorum* tended, on average, to probe the highest number of florets per flower head, while *A. mellifera* and *B. pratorum* moved more frequently between heads. There was no significant difference between honeybees and bumblebees in the average number of florets probed per flower head (however, see Fig 4.2iv).

Bee species	N	Mean no. florets per inflorescence	SE	Mean of minimum no. florets per flower	Mean of maximum no. florets per flower
A. mellifera	6	2.27	+/- 0.29	1.5	3.5
B. hortorum	21	5.38	+/- 0.90	1.4	17
B. lapidarius	38	4.14	+/- 2.08	1.8	11.7
B. lucorum	47	4.32	+/- 2.12	1.2	9.8
B. pascuorum	14	2.86	+/- 1.47	1.0	6.3
B. pratorum	5	2.32	+/- 0.39	1.0	6.3
B. terrestris	2	5.05	+/- 3.55	1.5	8.6
Bumblebees	127	4.22	+/- 0.23	1.0	17.0

Table 4.2 Mean numbers of florets probed per *Phacelia* inflorescence by seven bee species. Each datapoint within the samples refers to a sequence of flower visits (2-18 inflorescences) by an individual bee. N = sample size.

Linear regression analysis suggested a significant positive association between the incidence of probing per inflorescence and FVR ($p = 0.000$, $R^2 = 16.3\%$, $N = 123$). Higher flower visitation rates were associated with a higher incidence of probing across all bees foraging on the *Phacelia* crop (see Fig. 4.2iii). When a greater number of florets are probed per inflorescence, the flight time component of foraging is

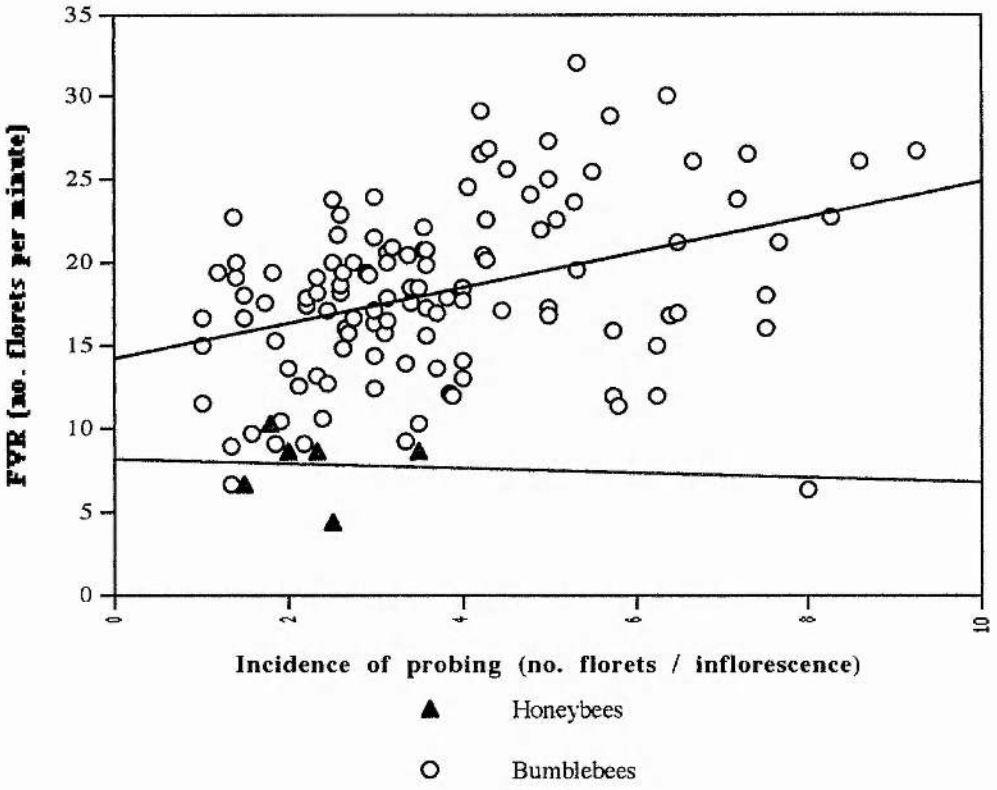
reduced and more individual florets can be sampled within a given time interval. The incidence of probing, however, is likely to be influenced by mean nectar rewards within that time interval.



No. florets / minute = 1.235 (no. florets / inflorescence) + 13.189

Fig. 4.2iii The association between FVR (mean number of florets probed per minute by an individual bee) and the mean number of florets probed per minute. N = 123.

When the data are examined separately for honeybees and bumblebees, two different relationships are suggested by the form of the graph (see Fig. 4.2iv). Whereas bumblebees' FVRs increased with an increase in the incidence of probing, the opposite appeared to be true for honeybees. The data showed no significant effect of mean nectar volume or concentration on the incidence of probing, despite the associations suggested by Figs. 4.2ii and 4.2iii.



FVR (Bumblebees) = 1.057 (no. florets / inflorescence) + 14.278

FVR (Honeybees) = -0.129 (no. florets / inflorescence) + 8.116

Fig. 4.2iv The association between FVR and incidence of probing for honeybees and bumblebees on *Phacelia*. N [bumblebees] = 117; N [honeybees] = 6.

4.3 The size and species composition of the bee community on *Phacelia*

4.3i The *Phacelia* community

The community of bees foraging on *Phacelia* between 19/7-28/7/95 was composed of the following species (listed in decreasing order of number of total observations during all timed walks): *B. lapidarius*, *B. lucorum*, *A. mellifera*, *B. pascuorum*, *B. hortorum*, *B. pratorum* and *B. terrestris* (Fig 4.3i).

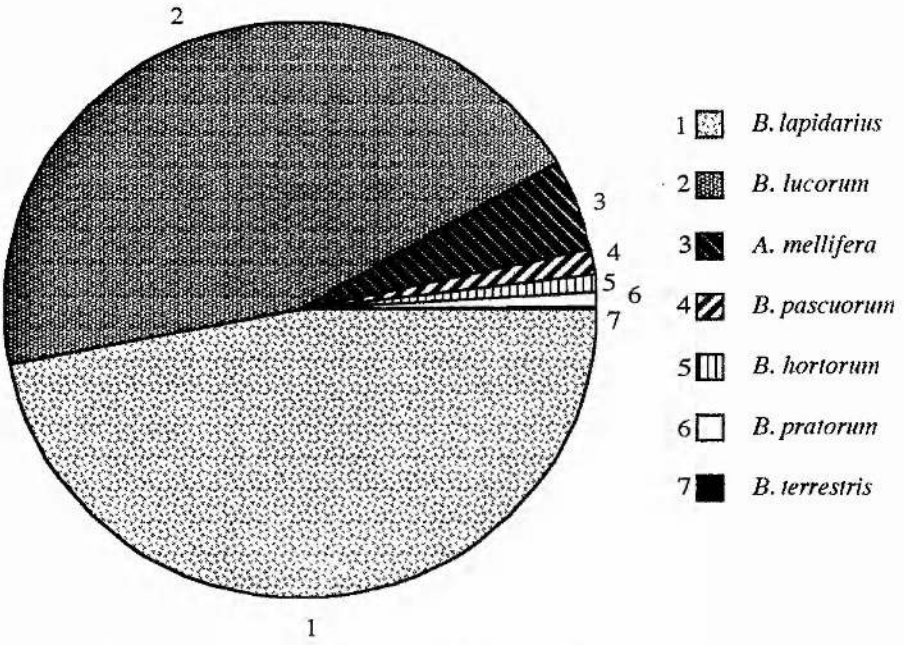


Fig. 4.3i Relative abundance of bee species foraging on *Phacelia* 19/7-28/7/95.

Other insects were present in small numbers on the *Phacelia* crop. These included various flies (Diptera, Syrphidae and Tipulidae), butterflies (Lepidoptera, Pieridae) and microlepidoptera, wasps (Hymenoptera, Vespidae), beetles (Coleoptera, Cantharidae) and leafhoppers (Hemiptera).

4.3ii *B. lucorum* and *B. lapidarius*: numerical dominance in the *Phacelia* bumblebee community

B. lucorum and *B. lapidarius* were the most abundant species on *Phacelia*. Fig. 4.3i shows that, overall, *B. lapidarius* was the most frequently recorded during timed walks. This, however, was not always the case. Data collected on two full separate days (26/7 and 28/7/95) highlight a shift in the relative abundance of these two species throughout the day.

Some bees were present in the *Phacelia* crop at 06:00 hours BST. At first, most were quiescent on the flower heads and appeared to have spent the night clinging there, but there followed a rapid increase in the ratio of foraging to non-foraging bees. On 26/7 and 28/7/95, an average of 138 *B. lucorum* and 23 *B. lapidarius* were counted during a timed walk of 20 minutes duration between 06:00 and 06:20 hours. Of these individuals, a larger proportion of *B. lucorum* workers were foraging than *B. lapidarius* workers. On 26/7, 92% of *B. lucorum* individuals and 64% of *B. lapidarius* were foraging at 06:00 hours. The corresponding figures for 28/7 are 61% of *B. lucorum* and 18% of *B. lapidarius*. By 07:00 hours a high proportion of bumblebees were foraging. *B. lucorum* was foraging in the greatest numbers between 06:00 and 09:00 hours on 26/7, and between 06:00 and 08:00 on 28/7/95. No quiescent bees were recorded after 09:00 on 26/7 and 08:00 on 28/7. After these times, *B. lapidarius* was numerically dominant on the crop. This shift is illustrated in Fig. 4.3ii.

The number of bumblebees foraging on *Phacelia* continued to increase throughout the morning. Bees travelled to the crop, discernible by colour and fragrance over long distances, from all directions. Bumblebee activity peaked during the mid-afternoon, for example at 16:00 hours on 26/7, and declined thereafter until 20:00 on 26/7 and 21:00 on 28/7. During the early evening, *B. lapidarius* numbers fell away more rapidly than *B. lucorum*, and between 18:00 and 21:00 hours *B. lucorum* was again the most abundant forager. Individual bumblebees ceased foraging from 19:00 onwards on both days. At 20:00 hours on 26/7, 28 *B. lapidarius* individuals (of which 71% were quiescent and clinging to flower heads) and 107 *B. lucorum* (of which 16% were quiescent) were recorded during a 20 minute walk. At 21:00 hours on 26/7, 31 *B. lucorum* foragers were recorded, but no foraging *B. lapidarius*. After 21:30 there was no evidence of bee activity in the field (see Fig. 4.3ii). Fig. 4.3iii shows the numbers of individual foraging *B. lucorum*, *B. lapidarius*, *A. mellifera* and *B. pascuorum* expressed as percentages of the total numbers of foragers.

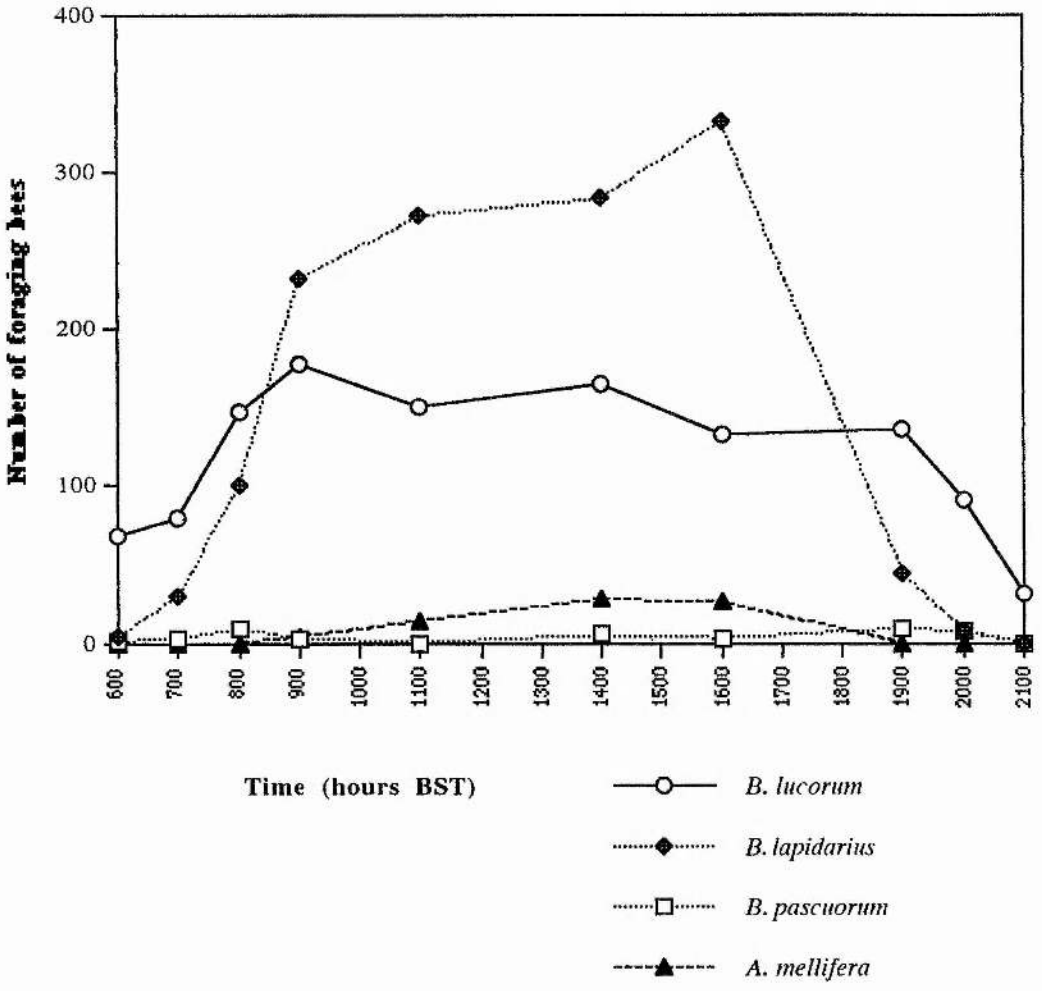


Fig. 4.3ii Numbers of individuals of *B. lucorum*, *B. lapidarius*, *B. pascuorum* and *A. mellifera* foraging on *Phacelia* on 26/7/95.

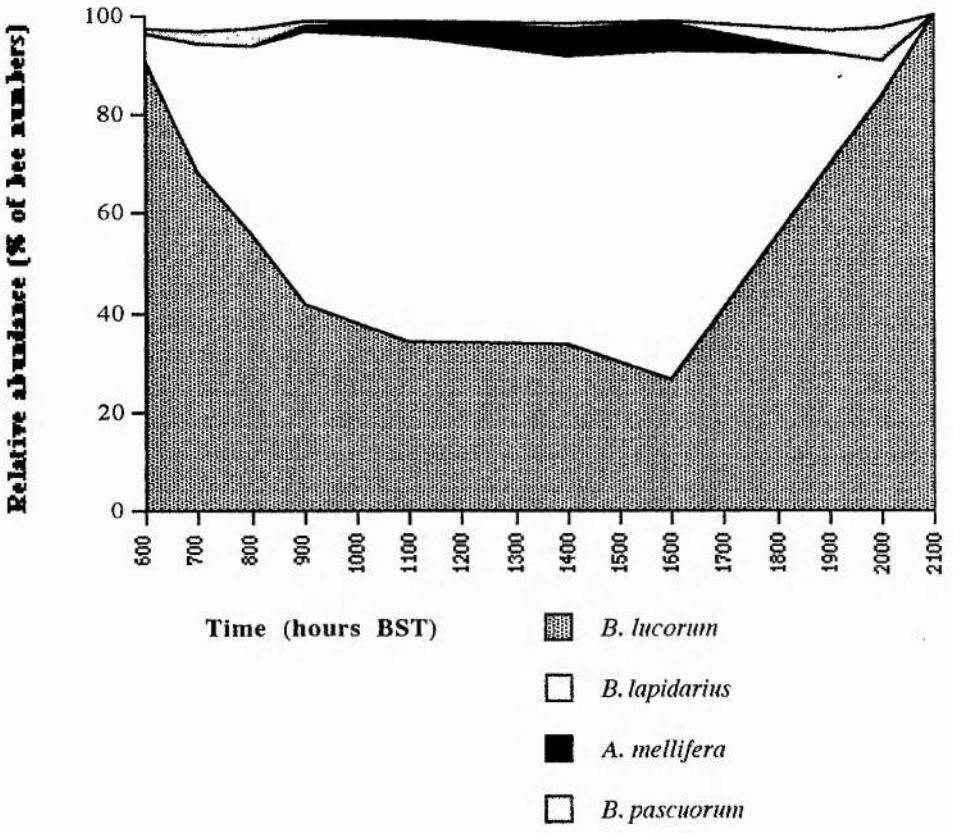
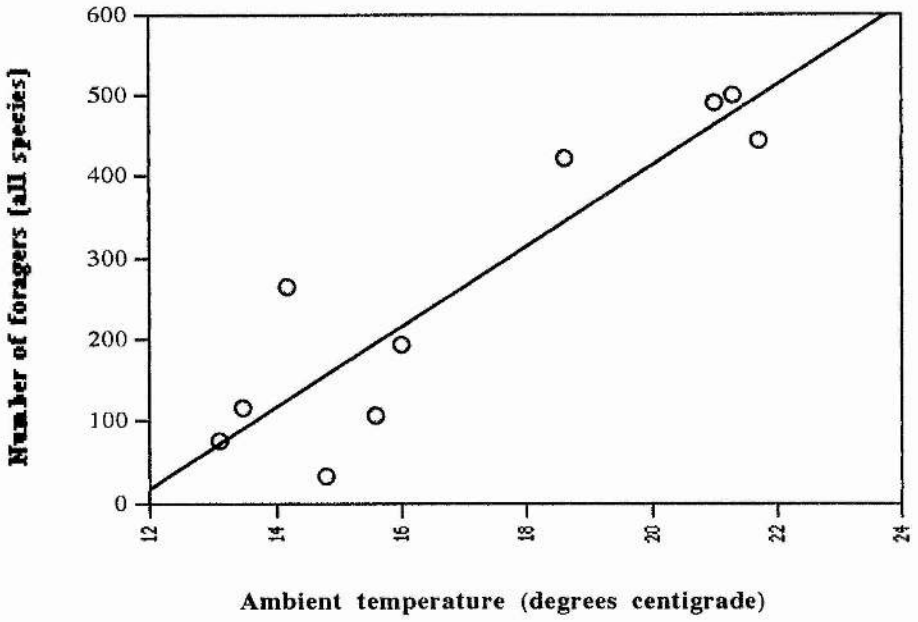


Fig. 4.3iii Relative abundance (percentage of total) of *B. lucorum*, *B. lapidarius*, *B. pascuorum* and *A. mellifera* foraging on *Phacelia* on 26/7/95.

4.3iii Environmental correlates of shifts of numerical dominance

There was a strong and positive association between the numbers of foraging bees on the crop and ambient temperature ($p = 0.000$, $R^2 = 82.3\%$). This relationship is illustrated in Fig. 4.3iv.



Number of foraging bees = 49.524 (Ta) - 576.525

Fig. 4.3iv The relationship between ambient temperature - T_a - (°C) and the number of bees (of all species) foraging on *Phacelia* 26/7/95.

Ambient temperature had a significant positive effect on the numbers of foraging *B. lucorum* ($p = 0.037$, $R^2 = 43.9\%$) and *B. lapidarius* ($p = 0.000$, $R^2 = 86.9\%$), but the strength of the relationship differed between the two species. The activity of *B. lapidarius* on *Phacelia* appeared to be more dependent on ambient temperature than that of *B. lucorum* . In other words, *B. lapidarius* required a higher ambient temperature than *B. lucorum* to initiate foraging, as suggested by the steeper slope of the *B. lapidarius* regression line in Fig. 4.3v. The slope of the *B. lucorum* regression line is closer to zero. The more statistically significant temperature relationship of *B. lapidarius* was emphasised by the fact that *B. lapidarius* data are more tightly distributed around their regression line. These conclusions are supported by the R^2 values quoted above for the effect of temperature on the activity patterns of each species.

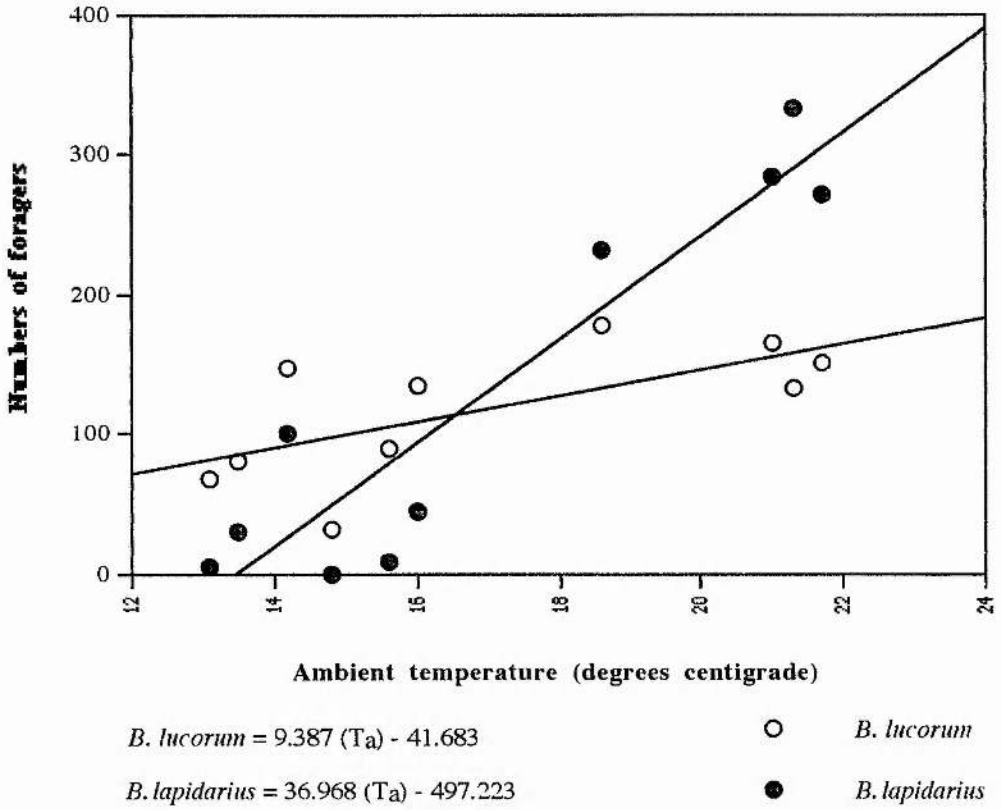


Fig. 4.3v Numbers of *B. lucorum* and *B. lapidarius* foraging on *Phacelia* with ambient temperature (°C) on 26/7/95.

The shift in ecological dominance from *B. lucorum* to *B. lapidarius* occurred between 08:00 and 09:00 hours on 26/7 and between 07:00 and 08:00 hours on 28/7, and reversed between 18:00 and 19:00 in the evening. Climatic data for 26/7 and 28/7 suggest that the temperature threshold for these shifts lay between 15 °C and 18 °C.

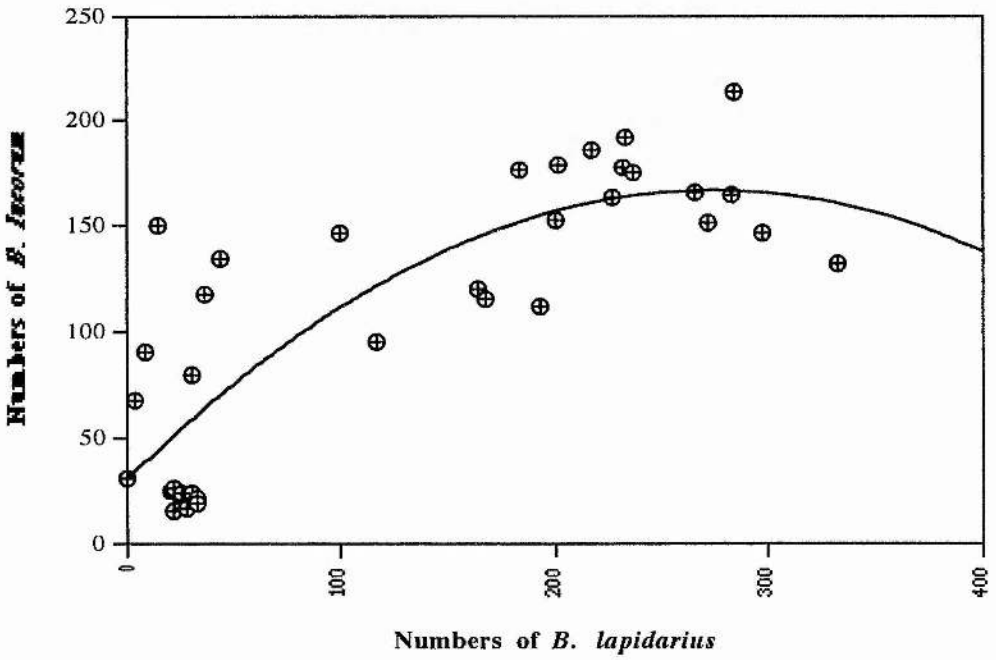
Fig. 4.3ii suggests that the increase in the numbers of *B. lucorum* levelled off after 09:00 hours, and even underwent a slight decrease. This corresponds to an earlier in crease in the numbers of foraging *B. lapidarius* workers. When numbers of *B. lucorum* are plotted against numbers of *B. lapidarius* over all days of the *Phacelia* study, the resulting graph suggests that there may be a critical density of *B. lapidarius* above which the numbers of *B. lucorum* begin to decline (Fig. 4.3vi). Linear

regression found a positive association between the absolute numbers of both species ($p = 0.000$, $R^2 = 63.8\%$), but this is because both species are significantly influenced by temperature. A second-order polynomial function supplies a slightly better fit ($p = 0.000$, $R^2 = 68.4\%$) and provides a more appropriate description of the data. Furthermore, when the data were divided into two groups according to the following relatively crude distinction:

i. No. of *B. lapidarius* ≤ 100

ii. No. of *B. lapidarius* ≥ 100

a significant difference was found in the numbers of *B. lucorum* ($p = 0.000$, $F = 18.35$), in the relative abundance (percentage of all observations) of *B. lucorum* ($p = 0.000$, $F = 84.19$), and in the ratio of *B. lucorum* to *B. lapidarius* ($p = 0.000$, $F = 40.18$) associated with each group.



No. of *B. lucorum* = -0.002 (*B. lapidarius*^{2}) + 1.000 (*B. lapidarius*) + 29.945

Fig. 4.3vi Numbers of B. lucorum foraging on *Phacelia* against numbers of B. lapidarius 19/7-28/7/95.

There are a number of possible explanations for this apparent relationship, including:

1. *B. lucorum* may be experiencing competition from increasing numbers of *B. lapidarius*, which are removing nectar at an ever-increasing rate;
2. *B. lucorum* workers may respond to increased numbers of *B. lapidarius* by direct avoidance strategies;
3. The decrease in *B. lucorum* may not be a reflection of *B. lapidarius*' competitive dominance, but may rather be a consequence of the relative sizes of the populations of the two species in the surrounding area; or,
4. The apparent effect may be due to the limitations of the observer in noting down the large numbers of bees at any one point (see section 2.2v).

In the final case, the data can be assumed to reflect the proportions of different bee species on the *Phacelia* crop, but not the absolute numbers of different species. The question of the reality of interference competition between these two species foraging on *Phacelia* is one for which the data contained in this thesis are insufficient, and requires consideration of the change in the nectar rewards of the crop over time. The nectar profile of the *Phacelia* crop was discussed in detail in Section 4.1. The following comments refer to observations regarding the influence of the nectar standing crop on the activity patterns of bees.

The volume and concentration of *Phacelia* nectar were tested separately for an effect upon the number of foraging bees (all species). Nectar concentration was a better predictor ($p = 0.008$, $R^2 = 71.4\%$) of total bee numbers than nectar volume ($p = 0.038$, $R^2 = 53.8\%$). Low nectar volumes and high nectar concentrations were associated with high levels of bee activity, and both sets of data were best fitted by an exponential function (Figs. 4.3vii and 4.3viii). A multiple regression model involving nectar concentration, nectar volume and ambient temperature as predictors accounts for more of the variation in the dataset ($p = 0.041$, $R^2 = 84.9\%$), however the direct effect of temperature on nectar itself needs to be taken into consideration.

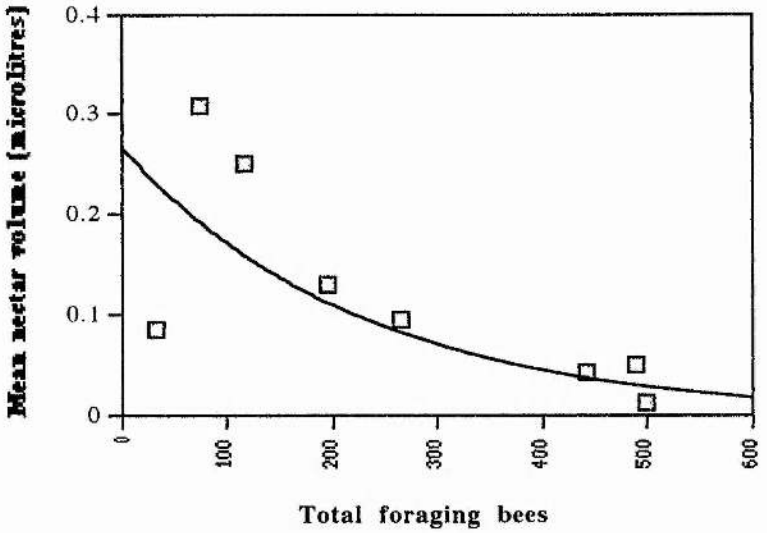


Fig. 4.3vii The relationship between nectar volume (μl) and the number of bees (all species) foraging on *Phacelia*, 26/7/95.

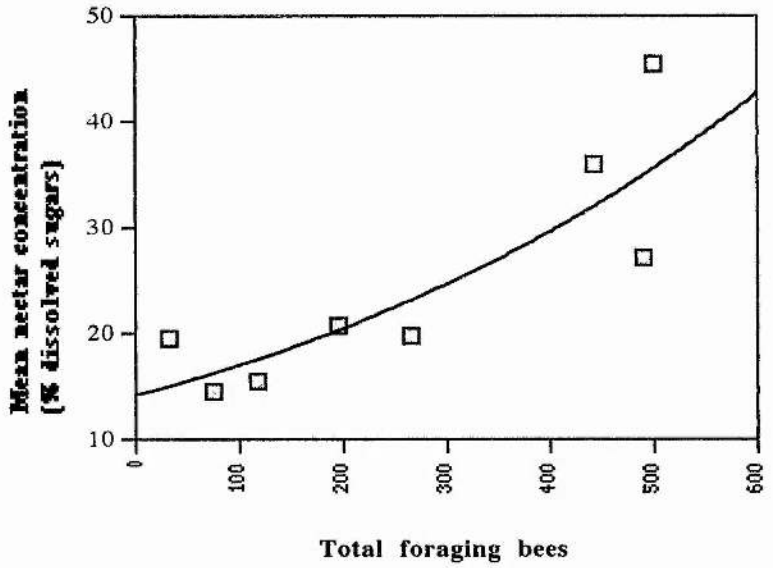


Fig. 4.3viii The relationship between nectar concentration (% dissolved sugar solids) and the number of bees (all species) foraging on *Phacelia*, 26/7/95.

If a multiple regression model of the same format is applied separately for *B. lucorum* and for *B. lapidarius*, a non-significant result is reached for *B. lucorum* ($p = 0.427$, $R^2 = 46.6\%$), while that for *B. lapidarius* is significant ($p = 0.013$, $R^2 = 91.6\%$). Likewise, *B. lucorum* data do not respond to either nectar concentration or nectar volume alone (or a model using both as predictors), while the *B. lapidarius* data show a significant effect both of nectar volume ($p = 0.033$, $R^2 = 55.8\%$) and nectar concentration ($p = 0.002$, $R^2 = 81.8\%$). This may be linked to the greater temperature dependence of *B. lapidarius*, since the characteristics of *Phacelia* nectar are strongly influenced by ambient temperature. On 26/7/95, *Phacelia* nectar volume decreased exponentially with increasing nectar concentration (see Fig. 4.3ix). When the numbers of both bumblebee species are plotted against nectar concentration (Fig. 4.3x), the slope formed by the *B. lapidarius* data is evidently steeper.

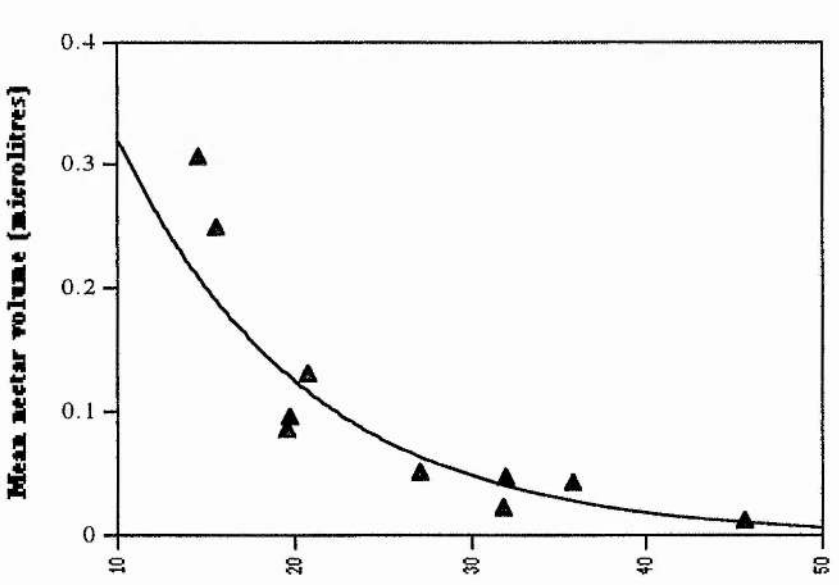


Fig. 4.3ix The relationship between mean nectar concentration (% dissolved sugar solids) and mean nectar volume (μl) on 26/7/95 in *Phacelia*. The data collected yielded the above equation.

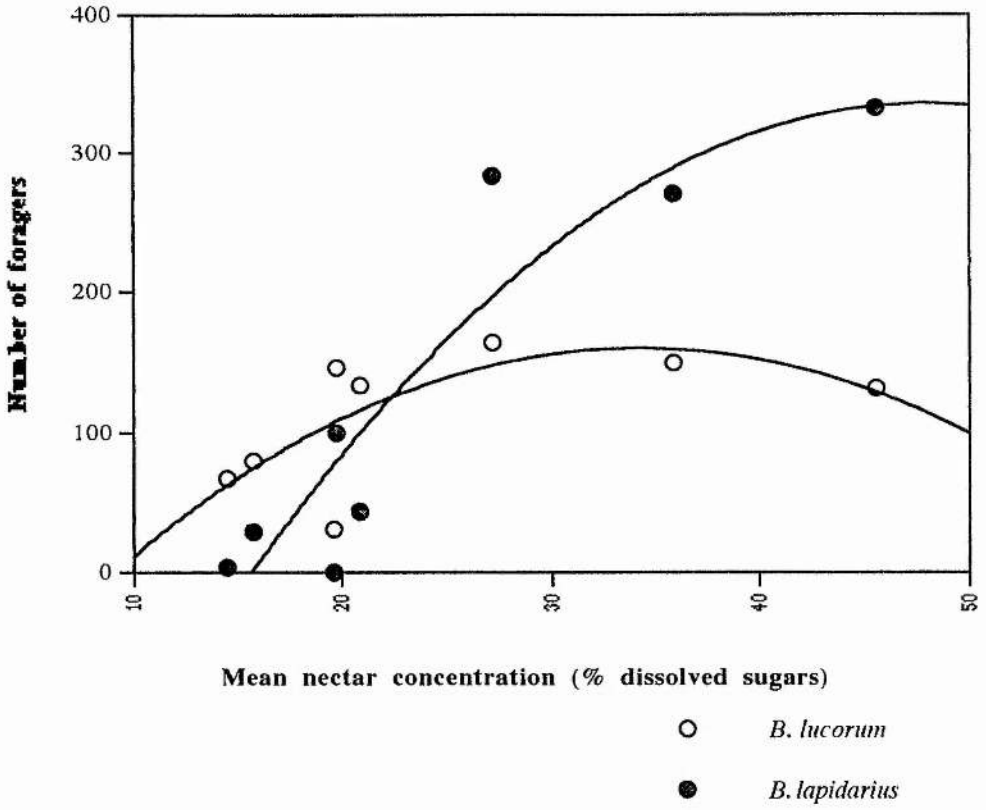


Fig. 4.3x The relationship between mean nectar concentration (% dissolved sugar solids) and the number of *B. lapidarius* and *B. lucorum* foragers on *Phacelia*, 26/7/95. Nectar volume decreases exponentially with increasing concentration, as expressed in Fig. 4.3ix.

4.3iii Activity patterns of *Apis mellifera* on *Phacelia*

At any time during the study there were relatively few honeybees foraging on *Phacelia*. On most occasions the number recorded during 20 minute timed walks did not exceed 30 individuals. One count of 60 was obtained on 27/7, on which day honeybees were consistently more numerous. On 26/7 the first honeybee forager was not observed until 09:00 hours, by which time ambient temperatures had reached 18°C. No honeybees were recorded after 18:00 hours on this day, at which point ambient temperature had fallen below 17°C. Changes in honeybee numbers and ambient temperature on 26/7 are illustrated in Fig. 4.3xi. Temperatures on 28/7 were

higher, and one *A. mellifera* was observed at 06:00 (ambient temperature = 16.5°C), with numbers increasing steadily thereafter.

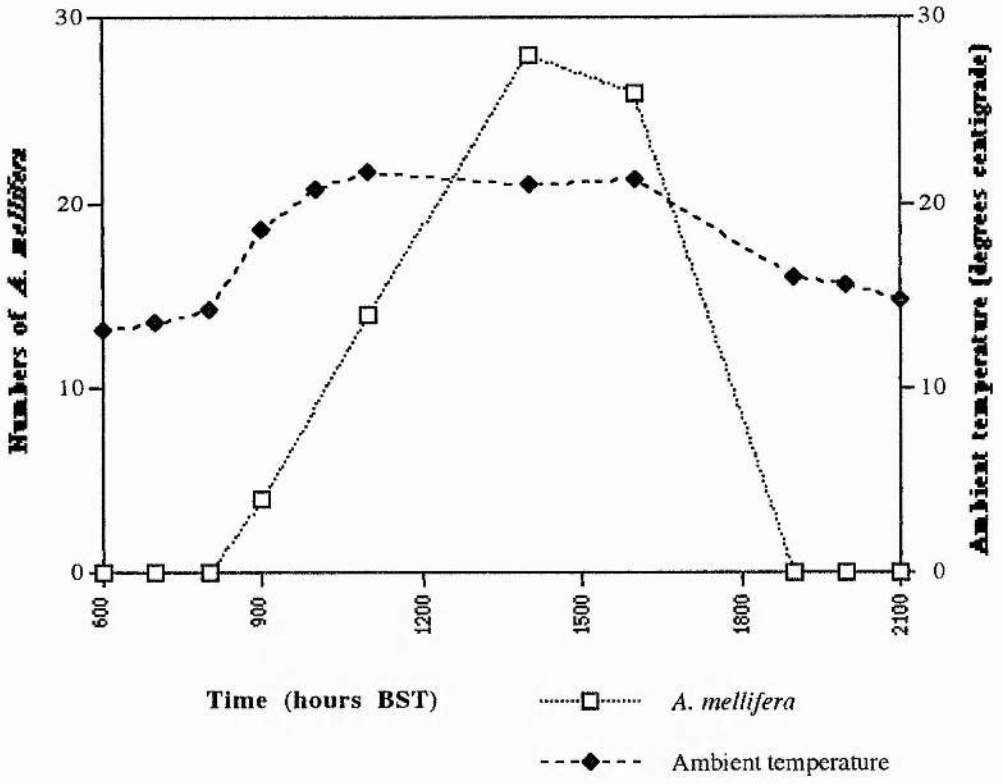


Fig. 4.3xi Numbers of *A. mellifera* on *Phacelia* and ambient temperature (°C) throughout the day, 26/7/95.

The data show a strong positive relationship between numbers of *A. mellifera* foraging on *Phacelia* and ambient temperature ($p = 0.000$, $R^2 = 75.0\%$). When honeybee numbers are plotted against temperature across all days of the *Phacelia* study, the resulting graphs suggests a temperature threshold for honeybee activity on *Phacelia* of approximately 17°C (see Fig. 4.3xii). This is to be expected if honeybees have a narrower thermal window for foraging activity than bumblebees. The interesting question of whether the relative rarity of honeybees on the *Phacelia* crop was due to competition from bumblebees is, unfortunately, beyond the scope of this study.

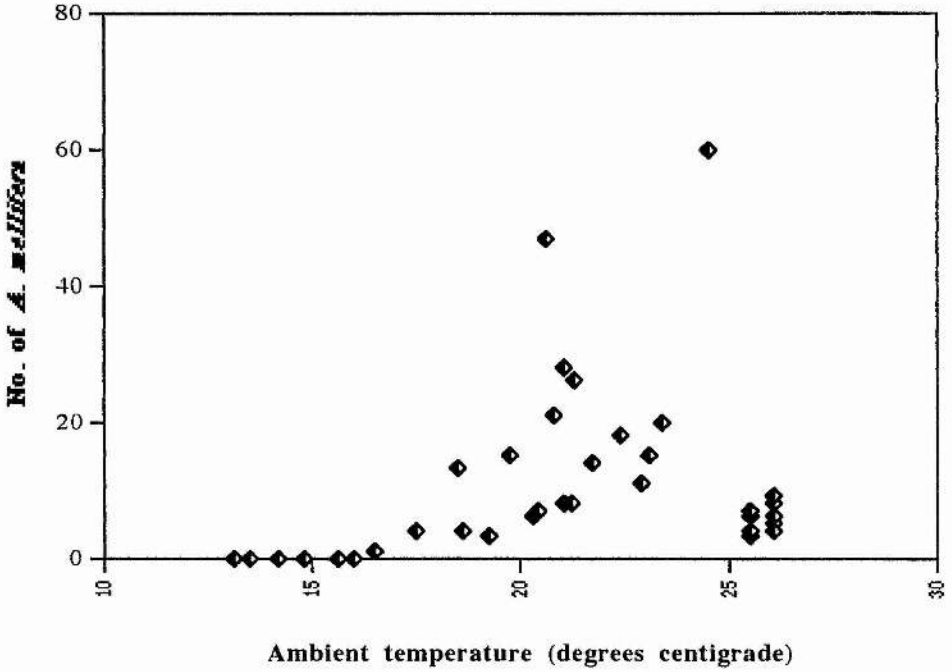


Fig. 4.xii Numbers of *A. mellifera* foraging on *Phacelia* with ambient temperature (°C), 19/7-28/7/95.

4.3iv Other species: *B. hortorum*, *B. pascuorum*, *B. pratorum* and *B. terrestris*

Other bumblebee species foraged in small numbers on the *Phacelia* crop. Of these, *B. pascuorum* was most frequently observed (although less common than *A. mellifera*), followed by *B. hortorum*; *B. pratorum* and *B. terrestris*, in order of frequency of observations. The activity patterns of these four species on *Phacelia* on 26/7 are illustrated in Fig. 4.3xiii.

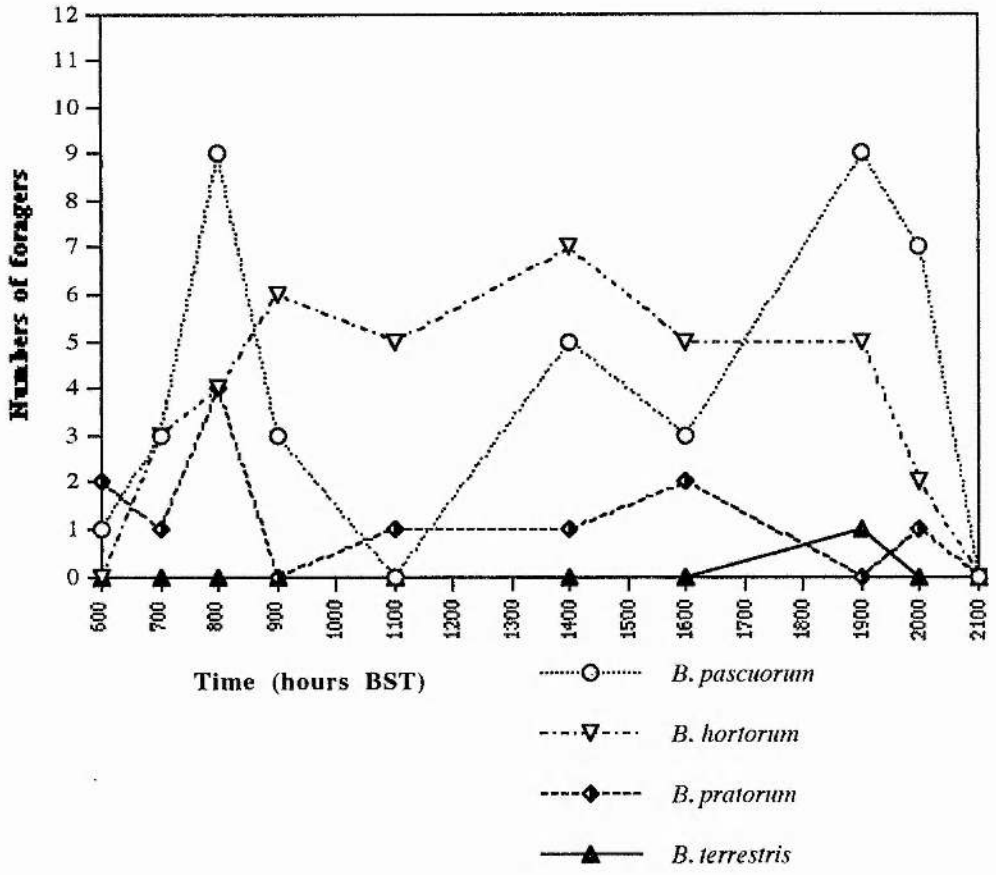
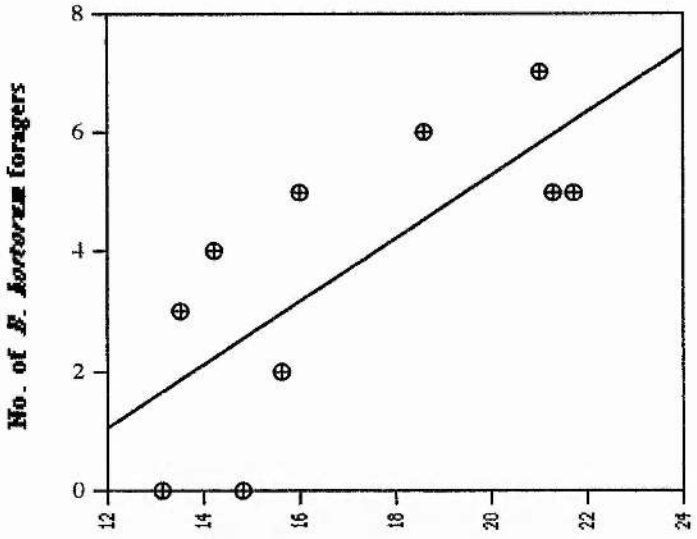


Fig. 4.3xiii Numbers of *B. pascuorum*, *B. hortorum*, *B. pratorum* and *B. terrestris* foraging on *Phacelia*, 26/7/95.

B. terrestris and *B. pratorum* were only seen in small numbers during the study. Two of the three *B. terrestris* individuals observed were large queens - probably the same individual. This suggests that *B. terrestris* workers were foraging at alternative nectar sources. Small numbers of *B. pratorum* were recorded on all days. On 26/7 two individuals were recorded at 06:00 hours; one at 07:00 and four at 08:00, after which numbers declined. On 28/7 the highest *B. pratorum* count was again obtained in the early morning (seven individuals at 07:00 hours).

Ambient temperature had a positive effect on the numbers of *B. hortorum* on the crop ($p = 0.015$, $R^2 = 54.4\%$). This trend is illustrated in Fig. 4.3xiv. No significant effect of nectar concentration or nectar volume was evident, however, the data suggest a

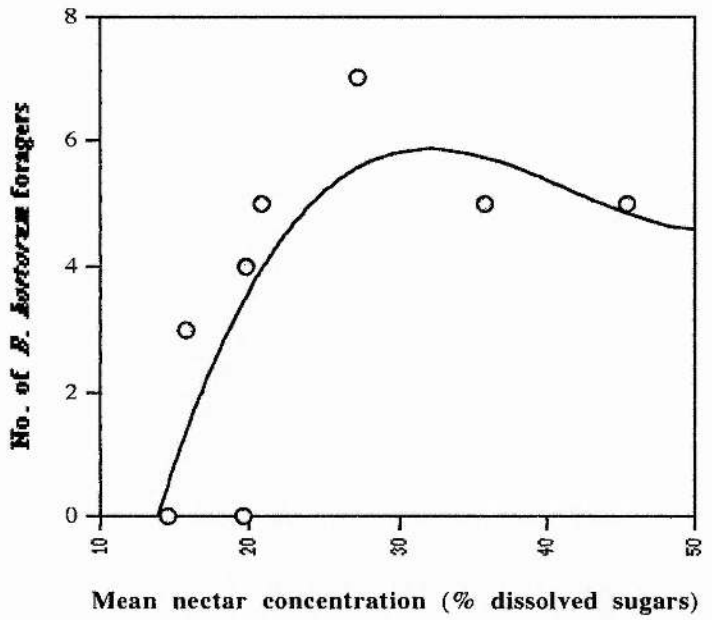
curved relationship which would require further data to substantiate (Fig. 4.3xv). A multiple regression model including the proportion of *B. lucorum* and *B. lapidarius* in the foraging population and ambient temperature as predictors, yielded a hypothesis accounting for much of the variation in the data. For 26/7, $p = 0.012$, $R^2 = 81.8\%$; over all days, $p = 0.003$, $R^2 = 34.5\%$).



No. of *B. hortorum* = 0.527(Ta) - 5.242

Fig. 4.3 xiv The relationship between ambient temperature (°C) and the number of *B. hortorum* foraging on *Phacelia*, 26/7/95.

B. hortorum was active in small numbers early in the morning (one at 06:00 hours, three at 07:00 and four at 08:00 on 26/7), increasing during the morning to peak in the early afternoon (seven at 14:00 on 26/7). None were recorded after 20:00 on 26/7 or 28/7.



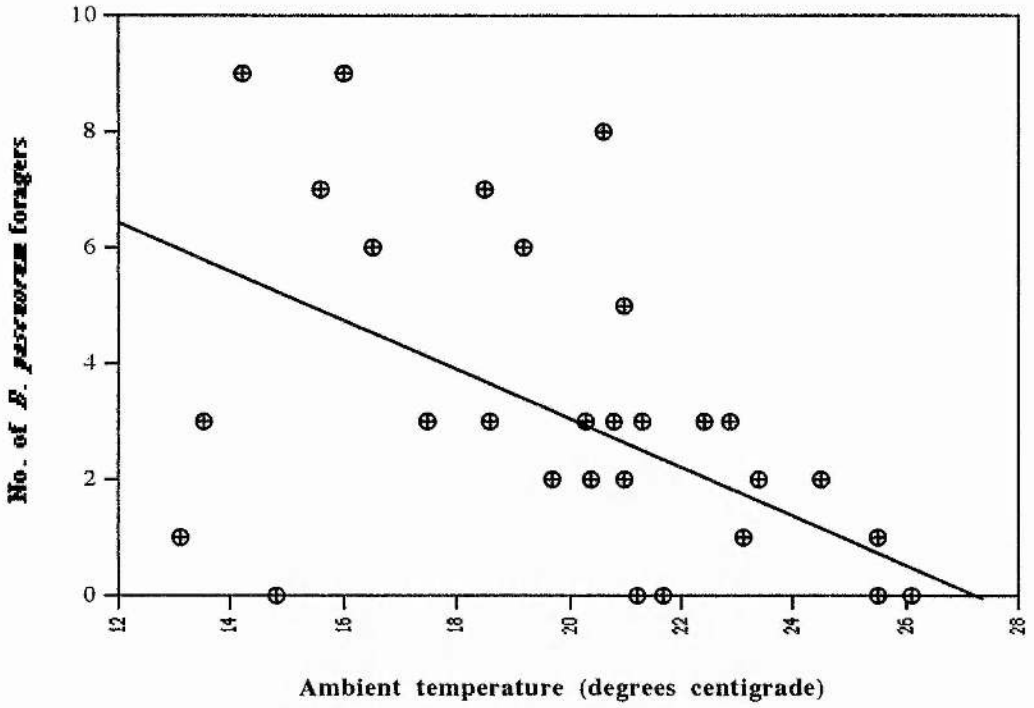
No. of *B. hortorum* = 0.000 (conc)^3 - 0.046 (conc)^2 + 1.836 (conc) - 17.451

Fig. 4.3xv Mean *Phacelia* nectar concentration (percentage dissolved sugar solids) and foraging by *B. hortorum*. A third-order polynomial has fitted as a possible description of the data.

Numbers of *B. pascuorum* foragers appeared to respond in an unusual way to ambient temperature. This is best illustrated by data collected on 26/7. Fig. 4.3xiii shows a bimodal pattern for *B. pascuorum* foraging. After 08:00 hours (ambient temperature = 14°C) *B. pascuorum* foraging declined, and rose again during the afternoon until 19:00-20:00 (ambient temperature = 15-16°C), when numbers peaked again. The average temperature for peak foraging of *B. pascuorum* on *Phacelia* can thus be estimated at around 15°C. Regression analysis yielded significant results for a negative linear ($p = 0.000$, $R^2 = 36.8\%$) and second-order polynomial ($p = 0.000$, $R^2 = 44.3\%$) effect of temperature on *B. pascuorum* numbers (see Fig. 4.3xvi). There is more variation in abundance at lower ambient temperatures (T_a) than at higher T_a, where numbers tend towards zero. Possible explanations for this include:

1. Physiological reasons: *B. pascuorum* may be more liable to overheat at high ambient temperatures than other bumblebee species, or,
2. *B. pascuorum* may be outcompeted on *Phacelia* by the ecologically dominant *B. lapidarius*.

A further possibility arises from the fact that small individuals of *B. pascuorum* were frequently recorded foraging on sheltered flowers during the middle of the day, when studies of flower visitation rates were taking place. Because of this circumstance, *B. pascuorum* may have been more likely to be missed by the observer during species counts.



No. of *B. pascuorum* = -0.419 (Ta) + 11.456

Fig. 4.3xvi The relationship between the abundance of *B. pascuorum* foraging on *Phacelia* and ambient temperature (°C) between 19/7 and 28/7/95.

Chapter 5

General discussion

5.1 Nectar

5.1i Field beans

The nectar profiles discussed in Section 3.1 indicate that there may be significant differences in the quality and quantity of nectar, and in nectar secretion patterns, between field bean cultivars. Nectar sampling carried out during this project suggested that the cultivars Scirocco, Toret, Glacier and Gobo were the most "rewarding" in terms of nectar volume per flower; Caspar, Toret, Victor, Scirocco, Maris Bead and Bourdon yielded the highest concentration of sugars per flower; while the lowest frequency of "negative" samples was found in Scirocco. The frequency of negative samples tended to exceed 50% in the majority of samples (see Section 3.1i), and may or may not represent the proportion of flowers in the crop which were energetically unrewarding to bees. The movement of nectar through the column of the microcapillary and the movement of nectar along the bee's glossa are similarly dependent on capillary action, but the mobility and dexterity of the proboscis probably permits the bee to imbibe nectar from floral recesses that are inaccessible to, or in volumes smaller than are extricable by, the microcapillary. I have nevertheless made the assumption that the frequency of negative samples obtained by the experimenter may be considered as an indirect reflection of the distribution of the nectar standing crop, since small nectar rewards (or nectar rewards sequestered deep within the corolla) may extend the 'handling time' component of

each flower visited. Negative samples, in addition, provide an inverse index of levels of bee activity (see Fig. 3.1iv).

Flowers of the wild type of field bean *V. faba* var. *paucijuga* (also known as variety 172) gave the lowest mean nectar concentration and volume of all of the experimental cultivars, which was reflected in the observation that bees foraged on this variety in much lower numbers than elsewhere in the plot. The small flowers, weak stems and slight architecture of the wild type, as well as its greater vulnerability to extremes of cold and wet in the British climate (Gavin Ramsay, personal communication), provide one possible causative factor in the lower overall nectar reward, and suggest that throughout the centuries during which agriculturists have bred this plant, an increase in the robustness of nectar secretion has been linked to the achievement of increasingly higher seed yields. Cultivars of standard height, which include one of the standard agricultural varieties (Troy), were observed to yield slightly but significantly higher volumes and concentrations of nectar than either "dwarf" or tall varieties, suggesting that one of the disadvantageous aspects of concentrating breeding efforts on specialised plant architecture may be a slight reduction in the quality and secretion rate of nectar. It would be interesting to make a study of inbred field bean plants to establish whether inbreeding depression may influence attractiveness to bees and/or seed yield through the nectar profile. In any case, to confirm suggested variations in nectar productivity between cultivars and between architectural groups, and to investigate the extent to which the origin of such variations is genetic or environmental, more exhaustive nectar studies would need to be carried out under a range of climatic and cultural conditions.

Although ambient temperature and humidity were found to have significant effects on nectar concentration, the rate of secretion of field bean nectar did not appear to bear a straightforward relationship either to ambient conditions or to time of day (see Section 3.1ii). Neither was there a simple relationship between nectar volume and concentration, but this may be largely accounted for by concurrent secretion and depletion by foraging bees throughout the afternoon. Excluding bees from flowers by a large cage or net would have provided a more accurate assessment of the physical relationship between concentration and volume, but would not have reflected the dynamic relationship between the two variables encountered by bees foraging under "natural", i.e. unrestricted conditions. In the present study it was not possible to

exclude non-hymenopterous insect visitors from the bean flowers, therefore nectar depletion may have been influenced by other species. However, at all times the number of non-*Bombus* foragers on the bean plot was extremely low.

Several authorities (see Introduction) had indicated that bumblebees would only visit field beans in appreciable numbers between the hours of 16:00 and 18:00 in the afternoon, and that even then their numbers would be small. This was found not to be the case in the experimental study plot, where bees were very active on field bean flowers for the greater part of the afternoon. Hardly any nectar foraging took place in the morning, although bumblebees were observed to visit wild flowers growing in amongst the beans. This corresponds to the low mean volume of nectar per flower before 12:00 hours, and coincides with the particular progression of the stages of flower-opening in field beans. *V. faba* flowers are only fully open - and therefore only fully accessible to bees - from early afternoon until dusk. The diurnal progression of flower opening was observed in Scirocco and Caspar on 26/6/95, and can be summarised as follows:

Time (hours BST):	**Stage of flower opening:**
09:00	Flowers all fully closed
11:30	10% of flowers open in Scirocco
14:00	50% of flowers open in Scirocco; 40% in Caspar
16:00	80% of flowers open in Scirocco
17:00	all of mature flowers fully open in Scirocco
18:00	all of mature flowers fully open in Caspar
21:00	flowers beginning to close up
22:00	95% of flowers are closed

Nectar production in an individual flower, however, may be initiated before the flower actually opens. Positive nectar samples were frequently recorded from "ripe" buds, i.e. flowers which were to open for the first time on the following evening. Therefore the nectar in ripe buds was often available to robber bumblebees while remaining inaccessible to "legitimate" foragers. This complements the observation that nectar-robbing *B. lucorum* or *B. terrestris* did not appear to distinguish between open flowers and ripe buds at any one node. "Legitimate" nectar foragers would be

expected to differentiate between mature flowers and ripe buds despite the fact that both may have contained equivalent quantities of nectar: a small number of *B. hortorum* individuals, however, were observed (on 1, 6 and 7/7/95) to approach closed flowers and open ones without apparent discrimination until very near the point of touch-lighting on the corolla, which raises once again the question of the extent of any remote nectar perception capabilities in bees, and the degree to which any such capabilities may be influenced by stereotypic patterns of behaviour.

The mean volume of nectar in the crop underwent a gradual decrease throughout the field bean flowering season (Section 3.1iii). This coincided with increasing numbers of bumblebees observed to be visiting the plot. However, a significant obstacle to drawing conclusions about the interaction of flowering period (e.g. the early-flowering Scirocco vs. the late-flowering Punch), nectar production and bumblebee visits arises from the differences in colony cycle between species and from the possibility that colonies within the same locality may show preferences for different nectar sources at any time during the growth and reproduction of the colony, depending on which nectar plants are in flower in the area, on the energetic cost of distance or of competition, and on any specific or familial floral preferences of the bumblebees.

5.1ii *Phacelia*

Phacelia nectar was secreted at similar low volumes but was on average more dilute than *V. faba* nectar. Both plant species showed a high degree of variation in the distribution of the standing crop of nectar throughout the day (see Table 5.1i).

	Nectar concentration		**Nectar volume**	
	Mean	**SE Mean**	**Mean**	**SE Mean**
per *V. faba* flower (N = 558)	34.33%	0.342	0.09μl	0.004
per *Phacelia* floret (N = 859)	18.6%	0.541	0.12μl	0.009

Table 5.1i Average nectar characteristics of *V. faba* and *Phacelia*

Ambient conditions of temperature and humidity were found to be strong correlates of nectar characteristics, indicating that the secretion of *Phacelia* nectar coincides more strongly than that of field beans with diurnal changes in environmental variables. *Phacelia* florets are open well before 06:00 hours, and appear to secrete nectar throughout the daylight hours. Mean nectar concentration reached a peak and mean nectar volume reached its lowest point when ambient temperatures were greatest (see Section 4.1i). This would be expected both on the basis of the direct physical effect of temperature on nectar, and on the indirect effect through the temperature-related activity levels of the bees. As in the case of field beans, the highest frequencies of "negative" nectar samples were obtained during the periods of greatest activity by bees (Section 4.1ii).

Because of the open structure of the corolla, the warm weather and the high levels of foraging activity in the field, *Phacelia* nectar reached high concentrations during the middle of the day (Fig. 4.1v), occasionally exceeding 50 per cent dissolved sugar solids. However, in certain parts of the crop, florets predictably yielded less concentrated nectar. These were the florets of the smaller, lower-growing flower heads constituting the "understory" of the crop, and shaded by the taller "canopy" plants (Section 4.1iii). The small amount of gathered data relating to this phenomenon are insufficient to show whether, as may be suspected, these sheltered florets may contain significantly (if only slightly) greater volumes of the more dilute nectar than emergent flowers. Larger sample sizes would be needed to confirm this. On several occasions small workers of *B. pascuorum* were observed to forage predominantly on the sheltered flower heads. It is possible that this may be because the small volumes of highly concentrated nectar (see Figs 4.1iv & v) in emergent flowers were either inaccessible by their relatively shorter tongues (compared to larger workers of the same species) or did not contain enough moisture to meet their metabolic needs (Harder 1983; '85 & '86). On the basis of these observations and the findings of preliminary nectar sampling, it seems reasonable to hypothesise that differences between the characteristics of nectar in sheltered and emergent flowers may be, at times, sufficiently significant, consistent and predictable to influence the foraging strategies of individual bees.

5.2 Foraging patterns and flower visitation

5.2i Field beans

Of the three major flower visitation strategies in the field bean pollinator community, positive flower visits were by far the most frequently observed. From data gathered during two days of the study (see Table 3.2i) the following estimates of the distribution of foraging strategies among bee species were reached. All individuals of *B. hortorum* and *B. lapidarius* and the majority (99%) of *B. pascuorum* made positive flower visits. All *B. terrestris* and the majority (89%) of observed *B. lucorum* made negative, corolla-piercing visits (primary nectar robbing). The small number of observed *B. pratorum* individuals were taking nectar from pre-existing corolla piercings (secondary nectar robbing). The majority of honeybees (70%) made positive flower visits. A small percentage of honeybees (13%) made negative visits to the flowers. The remainder of the honeybee population (17%) observed during these two days were engaged in visiting the extrafloral nectaries.

On a few occasions honeybees were observed to experience significant mechanical difficulty in entering the flowers. In these instances it was impossible for the bee to overcome the resistance presented by the standard petal, or the flowers were too deep for the bee to find any reward; however honeybees were frequently observed to enter field bean flowers without hindrance. One authority has stated that field bean flowers are impenetrable to the mandibles of most races of honeybee (Synge 1947), therefore nectar-gathering honeybees when present on a crop tend to exploit the holes pierced by short-tongued bumblebees, but this is a generalisation. In the present study honeybees were observed to act in the capacity of both primary and secondary nectar robbers. The potential mechanical resistance presented to smaller species by the relatively tight, deep corollas may provide a partial explanation for the relative rarity of honeybee foragers on the field bean plot compared to bumblebees (see Figs 3.2ii & iii), and for the fact that only one solitary bee was observed to attempt (without success) to probe.

Extrafloral nectaries are an important component of the attractiveness of field beans to insects. On a number of occasions (particularly in the morning or in the afternoon on very hot days) wasps, honeybees and small *B. pascuorum* were observed flying or

crawling between the topmost nodes of the bean plants, collecting nectar from the undersides of the stipules (the bracts which enclose the developing leaves). Stipular nectar is secreted at lower volumes than floral nectar, and is slightly less concentrated due to the fact that the stipular nectaries are supplied by both phloem and xylem vessels, while the floral nectaries are supplied only by the phloem, which is richer in dissolved solids (Davies, Peterson & Shuel 1988). This may help to explain why bumblebees tended to ignore it as a source of energy, and why it was popular among honeybees and small *B. pascuorum* on hot days when evaporation and water-deprivation in the plants would have made the floral nectar highly concentrated. Small bumblebee workers may have resorted to the extrafloral nectaries on such days because floral nectar may have fallen below a certain threshold volume and/or risen above a certain threshold concentration for effective foraging (Harder 1986), making extrafloral nectar more attractive (see Section 5.1ii). The function of extrafloral nectar is uncertain: it may serve to recruit bees to the crop before flowering and to maintain their interest in the patch when floral nectar levels are low, or may even function as an equivalent of "sugar syrup" (Free 1962) which, when supplied to hives, promotes pollen gathering by honeybees and encourages cross-pollination. The latter hypothesis seems unlikely considering that honeybees tend to restrict themselves to one mode of flower visitation behaviour per trip (Free 1962 and 1992; personal observation) and that in many areas of the world honeybees are not the most important field bean pollen-vectors (Wafa & Ibrahim 1959). Whatever its precise function, extrafloral nectar is likely to play an important role in the reproductive strategy of field beans.

Nectar robbing was the least common mode of flower visitation behaviour on the plot, reflecting the minor positions occupied by short-tongued bumblebees and *A. mellifera* in the foraging community. The pattern of interflower movement for robbers was similar to that of "legitimate" foragers; a robber bumblebee tended to arrive mid-way up the stem of the plant, and began to bite holes in flowers at the node nearest to the point of landing. From then on she worked her way upwards, moving to the mid-point of another stem on approaching the topmost nodes. It was noticed that nectar robbers were more difficult to approach for close-up observation than bumblebees probing frontally (see also Brian 1957).

Estimates of flower visitation rates for bumblebees foraging on field beans were compared with figures obtained in previous studies (see Tables 3.2ii and 5.1ii). Unless stated otherwise, all of the data given below represent the mean duration of individual visits and flower visitation rates (mean number of flowers visited per minute) inclusive of flight time. In all studies mentioned below, honeybees took longer to probe flowers than bumblebees of any species, and long-tongued bumblebees (*B. distinguendus*, *B. hortorum* and *B. pascuorum*) and *B. lapidarius* are the most rapid foragers effecting cross-pollination. Poulsen (1973) found higher flower visitation rates for long-tongued bumblebees than in the present study, but his work was carried out under different conditions of climate and agriculture and in a different geographical area. The present study revealed no basis for significant differences between foraging rates of bees on different field bean cultivars. In any case it is probable that any influence of clonal variations in plant architecture or nectar secretion characteristics on flower visitation rates would be much smaller than the influence of the specific morphology, physiology and behaviour of the bee.

The time required to travel between nectar sources, i.e. that required for inter flower movements, is an important influence on total foraging time. As well as flights between individual flowers and plants in the course of a foraging trip, inter flower movements included flights between miniplots and the circuitous "reconnaissance" flights undertaken by many individuals. The fact that flowers were often rejected before probing, and even after the bee had made a brief landing on the flower, must be taken into account in considering the temporal element of inter flower movements. Occasionally the numbers of rejected flowers exceeded the number of probed or robbed flowers in any one foraging trip. Bumblebees observed on the plot in the morning (between 08:00 and 12:00 hours) tended to follow circuitous flight paths and to alight briefly on flowers without attempting to probe them.

The movement of bees between field bean flowers and inflorescences was consistent with patterns described by Pyke (1978). Foraging was initiated mid-way up the stem, followed by short upwards flights between adjacent nodes on the same plant, at each of which only a small proportion of flowers were actually probed (mean incidence of probing = 29% of the flowers at a node).

Species	Activity	Mean no. seconds per flower	Mean no. flowers per minute	Mean no. flowers visited per plant	Source
Honeybees	*positive*	11.9	5.0		Free (1962)
Honeybees	*positive*	14.0	4.3	**1.8**	Poulsen (1973)
Honeybees	*positive*	11.5	8.1		present study
Honeybees	*negative (secondary)*	8.0	7.5		Free (1962)
Honeybees	*extrafloral*	4.7	12.8		Free (1962)
B. hortorum	*positive*	5.8	10.3	**2.4**	Poulsen (1973)
B. hortorum	*positive*	7.0	9.8		present study
B. pascuorum	*positive*	8.6	7.0	**2.3**	Poulsen (1973)
B. pascuorum	*positive*	9.5	9.0		present study
B. distinguendus	*positive*	3.9	15.3	**2.7**	Poulsen (1973)
B. lapidarius	*positive*	7.0	9.8		present study
B. terrestris	*positive*	7.0	8.6		Poulsen (1973)
B. lucorum	*negative (primary)*	6.6	9.2		present study
B. terrestris	*negative (primary)*	15.0	4.6		present study
Bumblebees	*positive*	3.4*	17.7*		Free (1962)
Bumblebees	*negative (primary)*	6.5*	9.2*		Free (1962)

Table 5.1ii Rates of flower visitation and foraging for bees on field beans. Data from various sources. * These figures may exclude flight time.

Bees visited no more than two or three nodes per plant, and if they continued to forage in the same patch, they then moved to a nearby or adjacent plant. If the next flower to be visited was at the same node and was physically touching the previous

flower, bees would often crawl between the two. Larger individuals were more frequently observed to clamber between flowers than small ones; this movement was easier for larger individuals because of the wide angle of orientation of one flower at a node to the next flower at the same node. The average distance travelled between successive plants changed under the influence of extreme weather conditions. On hot dry days (e.g. 27/6) when nectar sampling suggested a patchy distribution of small volumes of highly concentrated nectar, bees made conspicuously longer flights between successive flower visits. This is consistent with Pyke's (1978) optimal foraging hypotheses concerning the movement of bumblebees between inflorescences, but unfortunately the data from this study were too sparse for a substantial argument on this point. It was noticed that bees tended to restrict bouts of foraging to within one cultivar rather than switching between two, even when foraging on the borders of adjacent miniplots. In general, bumblebees did not spend more than a few minutes in a patch before moving on to the next cultivar.

The time spent in non-feeding behaviours constitutes a further important influence on foraging visitation rates. For example, *B. pascuorum* occasionally made disproportionately long flower visits (remaining 62 seconds at one flower on 26/6), reinserting its proboscis several times and then "cleaning" the proboscis with the front tibiae. "Reprobing" and "cleaning" were frequently observed in *B. pascuorum* , *B. lapidarius* and *B. hortorum*, and may have been involved in the collection of pollen. Bumblebees frequently carried full pollen loads. *B. hortorum* and *B. pascuorum were* the two species most frequently observed to be carrying grey faba bean pollen in the corbiculae. Direct interspecific interactions were infrequent. Bumblebees occasionally displayed avoidance behaviour according to a "pecking order". This hierarchy appeared to be based on size within species (this was observed particularly in *B. hortorum* and *B. pascuorum*), and on some other factor (possibly aggressiveness) between species. *B. terrestris* and *B. lucorum* exhibited definite aggressive tendencies on approach, and queens were more aggressive than the workers. One *B. pascuorum* was seen to wave its mid-leg in threat against hoverflies (12/7). *B. lapidarius* was observed on several occasions, during the hottest part of the day, resting or "basking" on the surface of the bean leaves. Quiescent individuals were seen on one or two occasions in the early morning or late evening (from 18:00 hours) clinging to the flowers at the proximal end of a node. Towards the end of the

flowering season (from 10/7) male bumblebees began to engage in mate-searching behaviour in the plot.

5.2ii *Phacelia*

The main division between types of flower visits made by bees foraging on *Phacelia* was between nectar-gathering and pollen-collecting visits. *A. mellifera* and *B. pascuorum* were the only species observed to collect pollen deliberately rather than incidentally, "raking" over the anthers with the tibiae. Bumblebees of all species frequently carried full loads of blue *Phacelia* pollen. Otherwise the most salient interspecific distinction in foraging strategy of bumblebees on *Phacelia* was concerned with the timing of activity (see Section 5.3ii) and the fact that small individuals of *B. pascuorum* were frequently noted to move between the lower, sheltered flower heads where nectar was significantly less concentrated on hot days (see Section 5.1ii).

Because of the entirely dissimilar architecture of field bean and *Phacelia* plants, patterns of inter flower movement on *Phacelia* were of a separate order and may be compared to those discussed above (Section 5.2i). Bees tended to visit only a small proportion, approximately 29% of an average of 6.2 individual flowers in each field bean inflorescence, i.e. at each node, before moving to another inflorescence. Nodes were frequently approached and then "rejected". In a similar manner, most of the florets on a *Phacelia* inflorescence were ignored by bees, which tended to probe, on average, only 26% of an average total of 14.1 mature, open florets. The frequency of potentially "unrewarding" flowers, as estimated by the frequency of negative nectar samples, was comparable in both crops, particularly during the middle of the afternoon when the number of negative records within a sample could reach 90% at any one sampling interval for field beans (N[field beans] = 40 individual flowers and N[*Phacelia*] = 32 florets at intervals of 1-2 hours; see Sections 3.1i & 4.1ii), and this may account for the similar incidence of probing on the two crops.

Bees walked between flowers on the same inflorescence. They flew between inflorescences unless it was directly adjacent, in which case they "jumped", and unless it was physically contacting the present one, in which case they "crawled" or "climbed". Bees often crawled between adjacent flowers where flight would have

been much more rapid, but crawling avoids the need for the metabolically expensive muscular "shivering" of warm-up (Prys-Jones 1986). Prys-Jones argues that foraging on clustered flowers, such as *Phacelia*, on which the bee can walk between adjacent florets, requires long periods of non-flying when the thoracic temperature of the bumblebee may fall below that required for flight. In order to fly to the next flower, a temporal delay will be incurred by the necessity of shivering thermogenesis or "warm-up", which consumes energy at a rate similar to that expended during actual flight. This point, thrown into relief by patterns of inter flower movement dictated by the composite structure of *Phacelia* flowers, is of considerable interest to the discussion of species composition differences between the bumblebee communities of field beans and *Phacelia* (see Section 5.3).

As would be consistent with the numerical dominance of *B. lapidarius* and *B. lucorum* in the *Phacelia* community, these two species were found to have significantly higher rates of flower visitation (FVR, or mean number of florets probed per minute) than the long-tongued bumblebees *B. pascuorum* and *B. lapidarius* which constituted the major elements of the field bean community. The corollas of *Phacelia* are shallower than those of field beans: the mean total depth of a *Phacelia* floret was 11.3 mm from the margin to the base of the corolla, compared to a mean total depth of 28.9 mm for field bean flowers (all cultivars). This gave a mean functional corolla tube depth (i.e. the distance from the most distal point at which the tube formed by the corolla was continuous to the base) of 7.1 mm for *Phacelia* and 12.7 mm for field beans (all cultivars). In addition, *Phacelia* corolla tubes are narrower than those of field beans: the mean diameter at the midpoint of a *Phacelia* corolla was 2.0 mm compared to a mean diameter of 5.1 mm for the midpoint of the field bean corolla. These vital statistics further contribute to the ease of flower handling and the accessibility of *Phacelia* nectar to bees with shorter proboscides, as the access time element of flower handling time may be reduced (Harder 1983; see below). By far the most rapid forager on *Phacelia* appeared to be *B. terrestris*, but the number of this species observed was too small for reliable inference. Honeybees visited markedly fewer *Phacelia* florets per minute than bumblebees in general (7.8 florets per minute compared to 18.5 for bumblebees; see Table 4.1) but the figures obtained during the present study may have been confounded by the fact that the data were not separated, as would have appropriate, into visits for nectar and/or pollen.

FVR was shown to increase in a slight but significant degree with decreasing mean floral nectar volumes. Further studies might be expected to corroborate this apparent relationship since larger volumes of nectar in a floret may increase the ingestion time component of flower handling time (Gilbert 1981; Harder 1983) where:

flower handling time = flight time + probing time, and
probing time = access time + ingestion time

Because any potential time increment due to small increases in nectar volume is likely to be very small, large sample sizes would be needed for an undiminished argument. Harder (1983) argued that the relation of probing time to flower depth is an important influence on foraging efficiency and flower choice in bumblebees. The mean number of florets probed per inflorescence (the incidence of probing) was shown to be dependent on bee species (see Section 4.2iv). *B. hortorum* gave the highest estimate of probing incidence: 5.4 florets per inflorescence (N = 21) compared to 4.1 and 4.3 for *B. lapidarius* (N = 38) and *B. lucorum* (N = 47) respectively. If further investigation could confirm a predictable difference between the incidence of probing in these species, it would be worthwhile to consider it in the context of specific differences in their flight physiology, as "interspecific differences in thermogenic abilities [in bumblebees] may underlie observed differences in foraging ecology" (Prys-Jones, 1986).

The incidence of probing per flower head was significantly related to flower visitation rate (FVR), and the nature of this relationship differed markedly when data for honeybees and bumblebees were presented separately (Section 4.2iv; Fig. 4.2iv). The slope of the graph was much steeper for bumblebees than for honeybees, implying that FVR in honeybees is not primarily influenced by the incidence of probing. This effect, if real (and a larger sample size for honeybees would be needed to confirm it), could be linked to the observed tendency of honeybees to spend longer at each inflorescence in the process of collecting pollen. However, concrete data are lacking in this instance. Field observations suggested a tendency of bees to probe fewer florets per flower head and to travel farther between successive inflorescences during the mid-afternoon when ambient temperatures were highest. Under these conditions *Phacelia* nectar volumes were at their lowest and nectar concentrations at their highest, and any real extension of inter flower flight distances under these conditions

would support Pyke's (1978) application of Optimal Foraging Theory (Charnov 1976) to bumblebees.

5.3 Bee numbers and relative abundance

5.3i Field beans

In the present study, bumblebees were extremely numerous and were by far the most frequent and abundant insect visitors to *V. faba*. *B. hortorum* and *B. pascuorum* were the most abundant species, followed by *B. lapidarius* which underwent a significant increase in numbers towards the end of the field bean flowering season. *B. terrestris*, *B. lucorum* and *B. pratorum* were present in very small numbers, while *A.. mellifera* was only marginally more common. It is not possible at this stage to say whether the species composition of bees on the bean plot was representative of the local area or of the bee fauna that would be present in a large, commercial stand consisting of only one field bean cultivar, but the observations show an interesting accordance with Heinrich's (1976) statement that at any one time the number of bumblebee species at any one site is generally low, and that of these, only one or two will be conspicuously abundant.

Field beans receive most of their insect visitors during the afternoon (Stoddard & Bond 1987; Juliet Osborne, personal communication; personal observation). Whereas bumblebees begin to forage actively on other food plants early in the morning, very few visited the field beans before noon and none of these early visitors attempted to probe the flowers. This was to be expected considering the nectar profiles discussed in Sections 3.1 and 5.1. When nectar levels began to rise bee numbers increased significantly to peak around 16:00 hours (see Figs 3.3ii & 3.3iii). Although data on nectar production in the absence of depletion by bees was lacking, it seems probable that the mid-afternoon peak of bee activity represented the point at which mean nectar rewards (of which rate of secretion would be a determining factor) were highest. Furthermore, the peak in total bee numbers on field beans did not appear, on a daily basis, to be directly influenced by ambient temperature, although environmental variables may have had, overall, an influence on the numbers of bees foraging throughout the flowering season (Fig. 3.3iv). Field observations suggested a drop in

bee activity on very hot, dry afternoons (e.g. 28/6/95 when T_a reached 28°C between 14:00-15:00 hours), when mean nectar rewards were low (at 11:00 on 28/6, mean nectar volume was 0.0035 μl per flower at an average concentration of 62.66%, and by 14:00 any nectar in the flowers was too crystalline to permit sampling to continue).

The relative abundance of bumblebee species changed throughout the *V. faba* flowering season (see Fig. 3.3xv). When the early variety Scirocco was in flower, *B. pascuorum* was undoubtedly the most common bumblebee on the plot. As the mid-season flowering varieties (e.g. Frinebo and Toret) came into flower numbers of *B. hortorum* began to increase and exceeded those of *B. pascuorum*, which was still numerous. *B. hortorum* remained the most frequent visitor to the plot during the flowering of the late varieties (Maris Bead, Punch, Glacier and Bourdon) while numbers of *B. lapidarius* underwent a noticeable increase, a trend which might have continued had flowering continued further into the season. If the fluctuations in relative abundance apparent from the data are real, the spectrum of bumblebees visiting field bean cultivars would vary with clonal differences in flowering period. In any case, the findings contained in this thesis are highly dependent on the dates of flowering of the experimental cultivars.

B. hortorum is also known to be the main pollinator of faba beans in Southern Britain (Gavin Ramsay, personal communication). A number of factors may be responsible for the numerical dominance of *B. hortorum* on field beans. The one that springs most immediately to mind is the suitability of its very long proboscis for reaching the nectar in deep corollas. Glossa length is one aspect of a complex of morphological features, including body mass and wing length, which influence the foraging abilities and flower choices of bumblebees (Harder 1985). Morphological features, however, cannot be considered in isolation from ecological factors such as plant species richness, season and competition from sympatric species, or from the species' behavioural repertoire.

Perhaps the most fundamental influences on bumblebee foraging efficiency and flower choice are physiological. Prys-Jones (1986) has argued that "specific differences in the thermogenic abilities [of bumblebee species] are probably of equal or greater relevance [than tongue length differences] in reducing niche overlap", and suggests that the tendency of *B. hortorum* to specialise on single flowers is related to

the relatively low level of activity of the substrate cycling enzymes fructose diphosphatase (FDPase) and phosphofructokinase (PFKase), which generate heat without the need for metabolically costly thoracic shivering, in the flight musculature of this species. Single flowers such as those of field beans, which require a brief perching time and must be reached by short flights, allow less time for the thoracic temperature to fall between periods of flight. Repeated bouts of shivering thermogenesis between flights would reduce the potential net energy gain of the foraging trip. Prys-Jones found a highly significant positive correlation between the levels of PFKase and FDPase activity in the flight musculature and the tendency of bumblebee species to forage on massed flowers (see Figs 5.1i & 5.1ii).

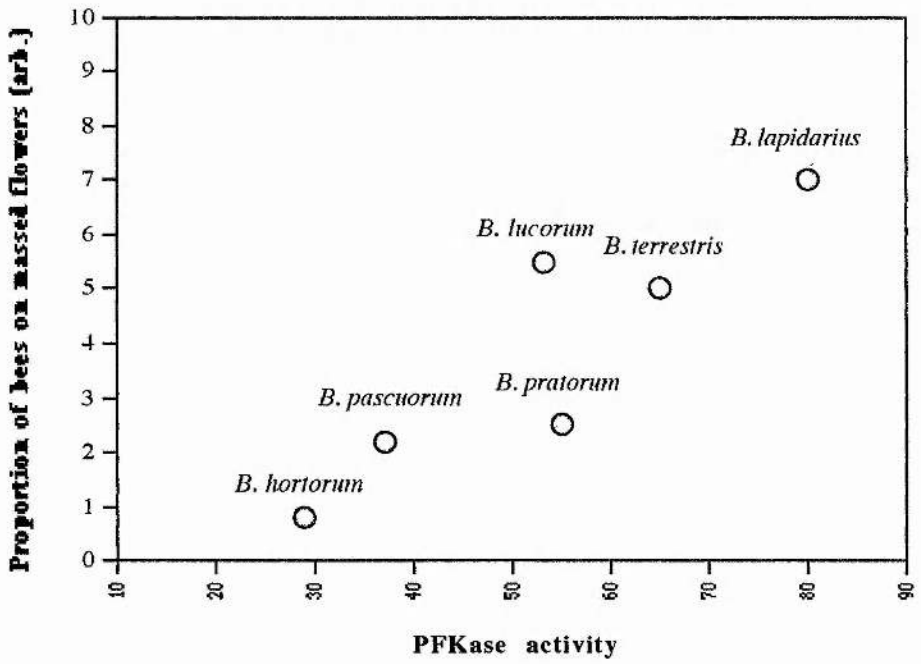


Fig. 5.2i The relationship between the activity of phosphofructokinase (PFKase) in the thoracic flight muscle (μmol min^{-1} g^{-1} muscle) and the proportion of individual bees of that species observed to forage on massed, as opposed to single, flowers (arbitrary units). Adapted from Prys-Jones (1986).

More than any other species, *B. lapidarius* was observed to respond to variations in ambient temperature in terms of absolute numbers of foragers and relative abundance of the species in the field bean community (see Figs 3.3ix & 3.3x). A similar effect

of temperature on *B. lapidarius* numbers was recorded on *Phacelia*, suggesting that this species is more dependent on ambient temperature for active foraging. *B. hortorum* was invariably the first visitor to the plot in the mornings and the last visitor at night (sometimes as late as 21:00 hours), while *B. lapidarius* was not recorded after 19:00 hours on any of the days on which a series of timed walks was carried out. Numbers of *A. mellifera* were also influenced by ambient temperature, but tended to be highest during the middle of the day. This may be due in part to the greater dependence of honeybee foraging on ambient conditions compared to bumblebee foraging, or it may indicate that the numbers of honeybees began to decrease during the afternoon as bumblebee numbers rose to a peak.

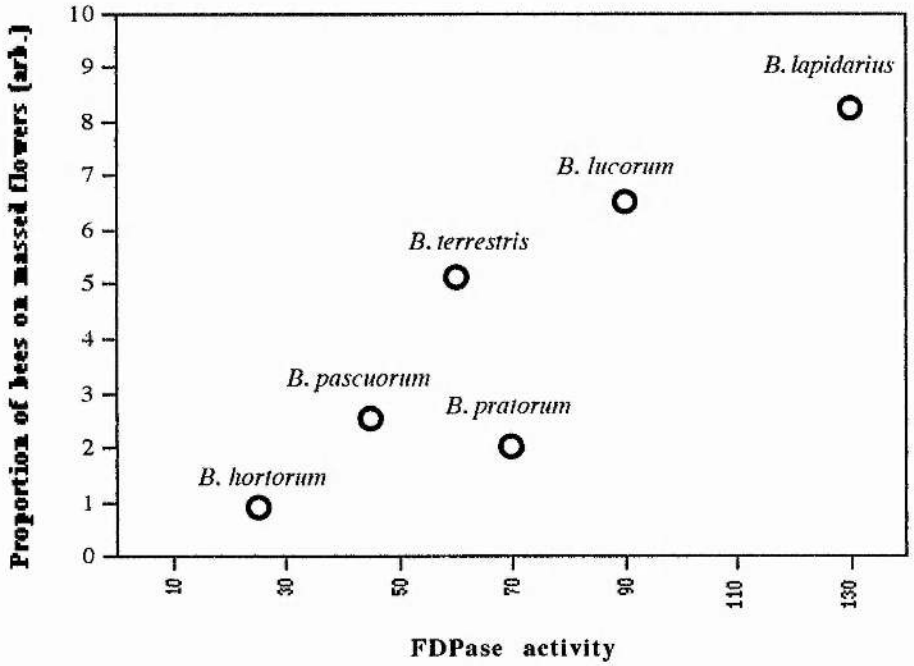


Fig. 5.2ii The relationship between the activity of fructose diphosphatase (FDPase) in the thoracic flight muscle (μmol min^{-1} g^{-1} muscle) and the proportion of individual bees of that species observed to forage on massed, as opposed to single, flowers (arbitrary units). Adapted from Prys-Jones (1986).

There was no indication that one or more of the field bean cultivars was preferred by any one or more species of bumblebees. This may partly reflect the fact that studies of relative abundance across cultivars were confined to a short period of 5 days (10-

15/7/95) when the four late cultivars (Bourdon, Glacier, Maris Bead and Punch) were in full flower. Field observations suggested that bumblebees visited Glacier and Maris Bead in greater numbers than Bourdon and Punch. It would be interesting to pursue this question, since Maris Bead and Glacier each had a higher floral density than Bourdon or Punch: Bourdon and Punch had, respectively, a mean floral density of 223 and 180 mature flowers per cubic metre at peak flowering, while the figures for Maris Bead and Glacier were 336 and 380 flowers per m^3 respectively. Analysis of variance, however showed these figures to be statistically insignificant ($p > 0.05$). There was no significant variation in the species composition of foragers on different cultivars. Despite the negative outcome of these investigations, it is feasible that a study on a larger scale (one, for example, encompassing two or more commercial crops within the same agricultural region) may go further towards establishing whether there is in fact a difference between the attractiveness (based on flower size, clone-specific characteristics of nectar secretion and/or differences in floral density) of field bean cultivars to bumblebees.

5.3ii *Phacelia*

The bee community foraging on *Phacelia* was comprised of the same species as the field bean community but in strikingly different proportions (see Section 4.3i). *B. lapidarius* and *B. lucorum* were the most abundant foragers, but which one was numerically dominant was dependent on the time of day. *B. hortorum* and *B. pascuorum* were only present in very small numbers (Fig. 4.3i). The first foragers to be active in the early morning were *B. lucorum*; *B. lapidarius* became active approximately one hour later (Fig. 4.3ii) and ceased foraging approximately one hour earlier than *B. lucorum* in the evening. During the intervening period, however, *B. lapidarius* were present in such large numbers that they accounted for the majority (49%) of all observations carried out (Fig. 4.3i). This pattern raises two interesting points.

The first is concerned with the arguments of Prys-Jones (1986) and research carried out during the early '70s which demonstrated variation in the capacity of *Bombus* species for thermogenic substrate cycling due to varying levels of FDPase and PFKase in the flight musculature. The data crudely represented in Figs 5.2i & ii show that, of the common British species, *B. lapidarius* and *B. lucorum* have some of the

highest activity levels of substrate cycling enzymes; in other words these species have the greatest capacity for maintaining a sufficiently high thoracic temperature to initiate flight after relatively long periods of perching, without incurring the delay or the extra energetic expense of standard shivering endothermy. Prys-Jones carried out a study of the proportion of visits carried out by the six ubiquitous British mainland species to massed and single flowers and found that *B. lapidarius* made the most use of massed flowers, closely followed by *B. lucorum*. The energetic advantage conferred on these species when foraging on massed flowers by their capacity for "cheap" thermogenesis gives them an ecological advantage over the longer-tongued *B. pascuorum* and *B. hortorum* and helps to account for their dominant role in the *Phacelia* pollinator community. The small bimodal peak in *B. pascuorum* activity (Fig. 4.3xiii) supports the hypothesis that long-tongued bumblebees on *Phacelia* may be "outcompeted" through the superior thermogenic abilities of the two dominant bumblebees.

The relative abundance of the two long-tongued species on *Phacelia* may also have been influenced by the relationship between mouthpart morphology, corolla tube depth, flower-handling efficiency and net energetic reward (Gilbert 1981). Tongue length is only one of many factors influencing foraging efficiency in bumblebees, and has variable predictive value depending on the types of flowers visited and the competing foragers and flora (Harder 1985). Foraging efficiency is, however, improved when the length of the insect's proboscis corresponds to the depth of the corolla tube (Ranta & Lundberg 1980) of the flower at which it forages. *B. hortorum* and *B. pascuorum* may have experienced the shallower corollas of *Phacelia* as less rewarding than other sources of forage, since *Phacelia* florets contain on average less nectar than deeper flowers such as *V. faba*, and are exploited in the main by shorter-tongued *Bombus*.

The shift of numerical dominance on *Phacelia* from *B. lucorum* to *B. lapidarius* at a certain threshold temperature (estimated from the present study at around 16°C; see Fig. 4.3v), as well as the apparent temperature dependence of *B. lapidarius* numbers on field beans (Figs 3.3ix &x), have been linked to the recent northward expansion of this species' range and the considerable increase of recent recordings in Fife (Iain Couzin, personal communication). Investigations of the temperature relationships of *B. lapidarius* and other *Bombus* species in Northern Britain may contribute to a better

understanding of range expansion and contraction. Furthermore, interactions between pollinator population dynamics and environmental conditions could provide an index of the extent and consequences of short-term climatic fluctuation, using insect populations as a marker.

5.4 Note on field bean yields

The pod-set figures cited by Soper (1952) and Stoddard (1986a) for commercial crops of field beans in the UK are startlingly low compared to the levels of pod-set observed in the experimental plot for the present study. Most plants bore several pods on each node, frequently more than five, with an average of 3.93 seeds per pod (N = 50, selected across all cultivars). The cultivars Glacier, Gobo and Punch were among the most productive, although all cultivars except the wild type showed high seed yields. The high observed yields are compatible with the large numbers of bumblebees observed foraging on the study plot, and may suggest the importance of thriving bumblebee populations for effective pollination.

Conclusion

Studies of the nectar profiles of the twelve experimental cultivars of field beans support the hypothesis that there are clonal differences in the quantity and quality of floral nectar in *V. faba*. If "nectar production" is considered as a combination of the average observed nectar volume and concentration per flower for each cultivar, a plot of average nectar characteristics (see Fig. 3.1x) indicated that Scirocco, Victor, Caspar and Toret are the most "productive" cultivars for floral nectar. The wild type *V. faba* var. *paucijuga* is far less productive than the commercial cultivars sampled. It is possible that differences in nectar productivity may be associated with clonal variations in plant architecture and floral structure. Differences in nectar productivity should also be apparent in large commercial stands consisting of one cultivar only, so that highly nectar-productive cultivars such as Scirocco may be more attractive to pollinators and benefit more from their activity than less nectar-productive cultivars. Bee populations would also benefit from higher nectar rewards in areas of *V. faba* cultivation. Further research would benefit from a study of the nectar profiles of large commercial stands.

No significant differences were observed in the behaviour, activity patterns or species composition of the foraging community of bees on each of the twelve cultivars. This result, however, may be due to the constraints of the small experimental scale and the set-up within which the study was carried out. The systemic allocation and replication of treatment groups (i.e. architectural 'types') among subplots and the randomised distribution of individual treatments (i.e. varieties) within this arrangement meant that cultivars were grown in small adjacent patches. Bees tended to work within miniplots but also travelled with frequency and ease between one patch (i.e. miniplot) and another. For this reason, study of the bee communities of large, relatively isolated fields would be necessary to draw conclusions about the relative attractiveness to bees of different cultivars grown on a commercial scale.

The long-tongued bumblebees *B. hortorum* and *B. pascuorum* were by far the most frequent visitors to field bean flowers. *B. lapidarius* and *B. lucorum* were relatively infrequent, although the numbers of *B. lapidarius* were observed to increase throughout the flowering season. Numbers of *Apis mellifera* were continuously low.

On the experimental site, bumblebees were superior as pollinators in terms of numbers, the length of their activity period on the crop, and the number of flowers visited, on average, per minute. The level of pod-set in the experimental plot was high compared to figures cited for some commercial crops (see Introduction). This suggests that the encouragement of bumblebee populations in areas of *V. faba* cultivation may be of great value in promoting pollination and yield.

B. lapidarius and *B. lucorum* were by far the most abundant foragers on *Phacelia tanacetifolia*. *B. hortorum*, *B. pascuorum* and *Apis mellifera* were relatively infrequent. The numerical dominance of *B. lapidarius* and *B. lucorum* compared to the two long-tongued species was reflected in higher rates of flower visitation (see Table 4.1). Observed differences in the species structure of the field bean and *Phacelia* communities may be explained by differences in floral structure between the two plants. The corollas of *Phacelia* florets are smaller and much shallower than *V. faba* flowers, suggesting decreased handling efficiency for long-tongued *Bombus* (Ranta & Lundberg 1980; Gilbert 1981). In addition, *Phacelia* flowers are borne on massed inflorescences while *V. faba* has spiked inflorescences in which the flowers at each node behave as 'single' flowers (in that short periods of flight are frequently necessary for inter-flower movement). For bumblebees foraging on massed flowers such as *Phacelia* there is a greater net energetic reward for those species possessing high activity levels of the substrate cycling enzymes FDPase and PFKase than for species with relatively low substrate cycling enzyme activity (Prys-Jones 1986).

In the early morning *B. lucorum* was the first bumblebee to be active on *Phacelia* and was numerically dominant until 08:00 or 09:00 hours BST. After this time numbers of *B. lapidarius* underwent a rapid increase and became the most abundant forager until between 18:00 and 19:00 hours BST when *B. lucorum* took over once again. These shifts took place at ambient temperatures of 16-17°C (see Fig. 4.3v), and are in agreement with previous findings that (despite its greater ecological dominance at ambient temperatures above 17°C) *B. lapidarius* has a higher temperature threshold for activity than *B. lucorum* (Corbet et al 1993).

The results of this small scale study support the value of field beans and of *Phacelia*, for example as cover crops on set aside land, for encouraging wild bee populations in agricultural areas. The observed differences in community structure suggest,

however, that deep corolla crops such as *V. faba* may be more beneficial to local populations of long-tongued bumblebees than *Phacelia* which (as stated in an advertisement for Semundo's 'Julia' variety in the Farmer's Weekly) is considered to "support bee populations" all round. Strategies for the conservation and management of British bumblebees would benefit from a survey of the bee communities on candidate 'pro-bumblebee' cover crops (such as *Phacelia*) in different agricultural areas within the UK.

Summary

1. Commercial cultivars of *Vicia faba* show significant differences in the volume and concentration of floral nectar when grown in small stands. Further work is necessary to establish the existence and extent of such differences in large commercial stands consisting of one cultivar only.

2. The behaviour, activity patterns and species structure of the foraging bee community was similar across all cultivars. This does not exclude the possibility that clonal differences in nectar productivity may be important for the pollinators of commercial stands.

3. The bee community on *V. faba* consisted of *Apis mellifera* and six species of bumblebees. The long-tongued bumblebees *B. hortorum* and *B. pascuorum* were superior as pollinators of field beans in terms of their numerical dominance, foraging speed (in terms of flower visits per minute) and the length of time during which they were active on the crop each day.

4. The bee community on *Phacelia tanacetifolia* consisted of the same seven species but in markedly different proportions. *B. lapidarius* and *B. lucorum* were by far the most active on the crop while the long-tongued *B. hortorum* and *B. pascuorum* were relatively scarce. These differences may be explained by differences in proboscis length (and ease of flower handling as measured by the mean number of flowers visited per minute) and/or interspecific differences in thermal physiology (as discussed by Prys-Jones 1986).

5. *B. lucorum* and *B. lapidarius* showed a shifting balance of numerical dominance on *Phacelia* throughout the day which appeared to be dependent on ambient temperature.

Appendix 1: Arrangement of experimental cultivars within the plot

Row	Column 1		Column 2		Column 3	
1	Frinebo	Troy	Caspar	Punch	Bourdon	Toret
	172	Glacier	Maris Bead	Victor	Scirocco	Gobo
2	Victor	Gobo	Maris Bead	Troy	Caspar	Glacier
	Punch	Toret	172	Bourdon	Frinebo	Scirocco
3	Glacier	172	Troy	Frinebo	Maris Bead	Victor
	Scirocco	Gobo	Bourdon	Caspar	Toret	Punch
4	Toret	Glacier	Punch	Caspar	Scirocco	Gobo
	Frinebo	Troy	Victor	Maris Bead	Bourdon	172

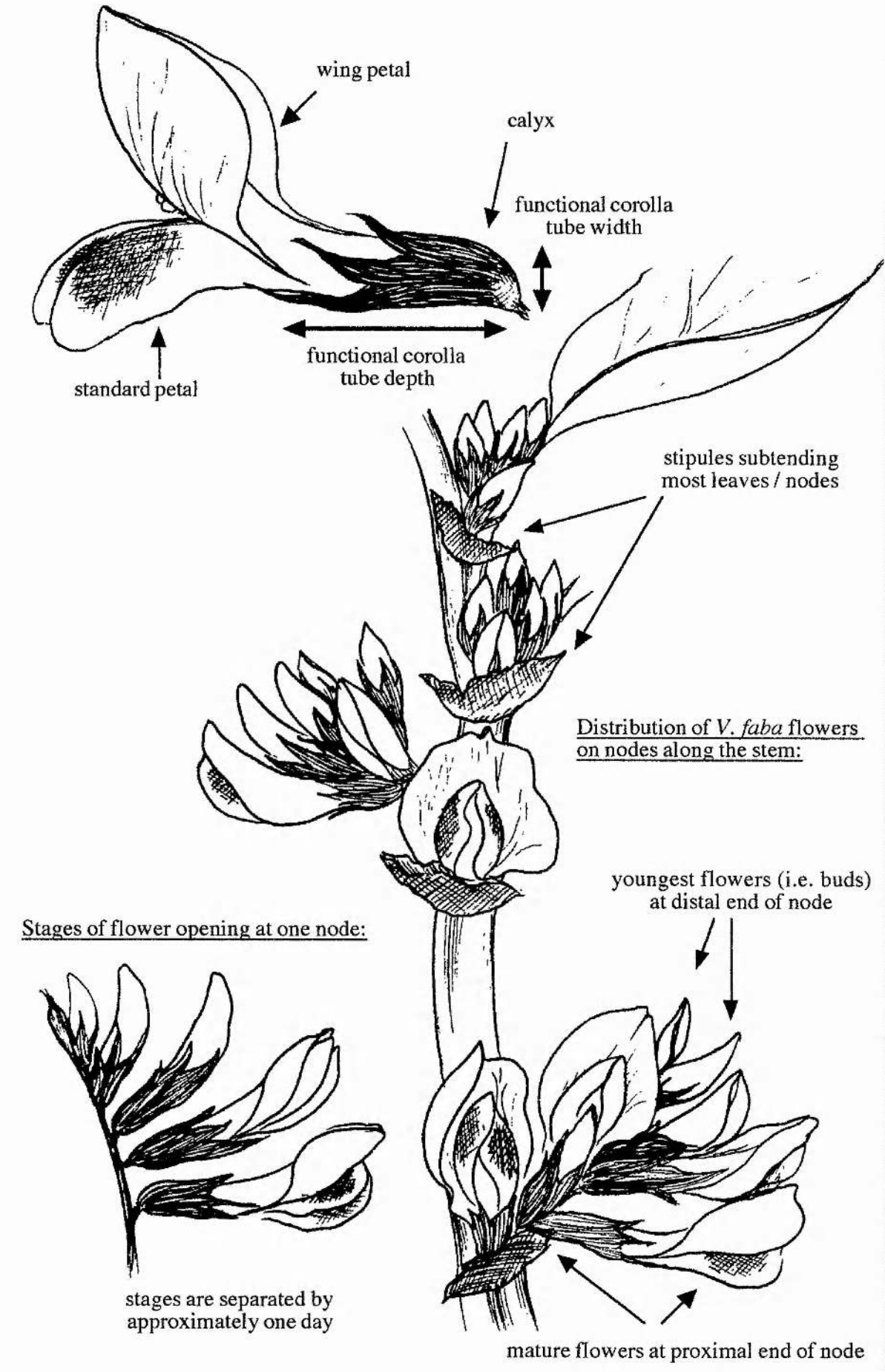
1 metre

1 metre

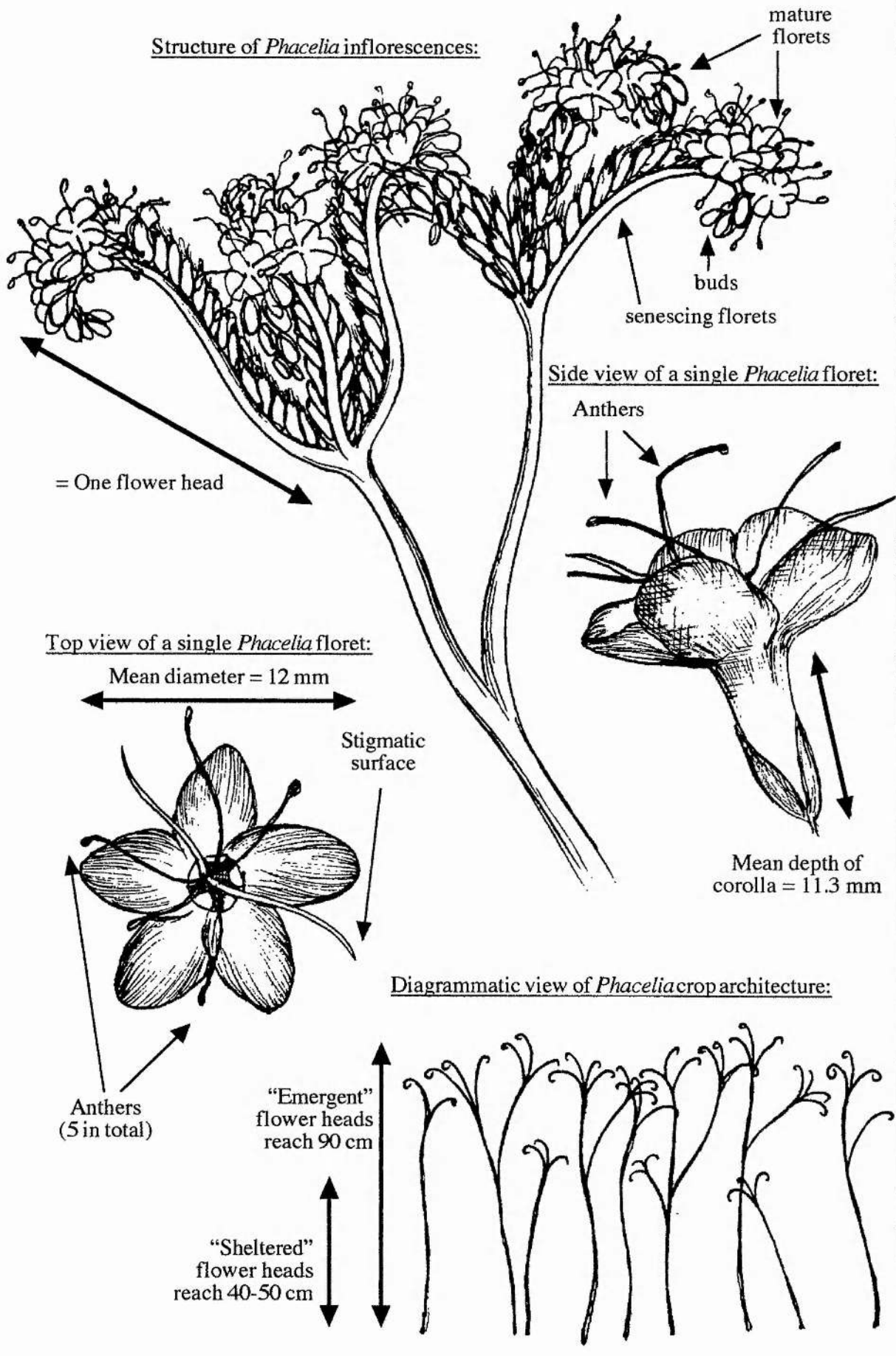
2.5 metres

2.5 metres

Appendix 2: *Vicia faba*



Appendix 3: *Phacelia tanacetifolia*



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Dedication

For Fiona Elly King and Daniel William Griffin.

Ode
in honour of *Bombus hortorum*, Linn.

No creature hath been blessed with Grace like she;
Serene from dawn to dusk, and ne'er uncouth,
She stoopest not to rage or petulance,
Nor once hath broke her poise to buzz at me.

Her onyx eyes fix on uncharted worlds
Too small and bright for human eyes to see;
Her tarsi tread sweet ballet in the air,
Her furlèd glossa lovelily uncurls.

The gentle patience held within her gaze
(so expressive of the psyche of a bee),
Inspired this offering of purple prose,
(as well as Homer's muse in ancient days).

No other bee should dance among white clover,
Nor sip the honeysuckle's golden bell.
Loud, brutal man will never guess the measure
Of the sad, sweet mysteries with which she dwells.